

Biodiversity, Community and Ecosystems

John Dighton
Jennifer Adams Krumins
Editors

Interactions in Soil: Promoting Plant Growth

 Springer

Biodiversity, Community and Ecosystems

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Editors

Interactions in Soil: Promoting Plant Growth

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Preface

In terrestrial ecosystems, soil is the rooting matrix in which plants grow. But, what makes for a good soil and what challenges are there for sustaining a soil for optimal plant growth? It is from this viewpoint that we have assembled the chapters in this book to describe the functional interactions of the organisms in soil that lead to soil quality. For most horticulturalists and agriculturalists, soil is a black box – the medium which supplies the plant with nutrients and water, to which fertilizers need to be added, on occasion, to maintain plant growth. However to the soil ecologist, soil is a living entity comprising of the mineral and organic matrix in which a myriad of life interacts with each other and with the plants growing there. This soil entity is a dynamic system with spatial and temporal heterogeneity making it one of the most complex of ecosystems. The complexity and biodiversity of organisms in soil is essential to the ecosystem services provided by soil and in maintaining homeostasis in the supply of nutrients for plant growth and suppression of plant pathogenic organisms. However, the disease suppressiveness of soil is challenged in the face of intensive agricultural practices, land use change, pollution and invasive species, which may suppress biodiversity and alter soil chemistry. Monocrop agriculture is more susceptible to pathogen attack than mixed crop or natural vegetation. Disturbance events reduce biodiversity and often leave a community less well adapted to protect plants from pathogens, and invasive species frequently change soil conditions to the dis-benefit of native vegetation, allowing competition by the invasive species to be enhanced.

This book originated from an interest in Dave Coleman's keynote address to the 6th Australian Soilborne Disease Symposium (Coleman 2011) in which he highlighted the importance of soil biodiversity in disease suppression as well as noting our lack of understanding of many components of soil that have received little investigation, including the role of viruses, trophic and non-trophic interactions regulating processes, soil management techniques and the increasingly important role that molecular tools may reveal in the functioning of microbial populations and communities. In this short book, we review and develop the idea that soil has both a suppressive and supportive role in plant growth. This is encompassed in soil biodiversity and the trophic and non-trophic interactions that occur within the soil biotic

community regulating the supply of nutrients to plant populations and communities. Much of the biotic interactions occur around the plant roots, so we explore the unique diversity of organisms in that zone, along with the plant pathogens that gain access via roots and investigate the effects of urbanization and invasive plants on these interactions as disturbance factors.

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Coleman DC (2011) Understanding soil processes: one of the last frontiers in biological and ecological research. *Aust Plant Pathol* 40:207–214

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Chapter 1

Introduction: Soils and Their Promotion of Plant Growth

John Dighton

Abstract Soil is a complex milieu of physical and biological entities that regulates the availability of nutrients for plant growth. The interactions between the elements of the soil biota and the plants during this process are complex and often rely on feedbacks between the plants and the great diversity of soil organisms that function to regulate processes to support plant growth. The rhizosphere and its mycorrhizal component are important parts of the connection between the plant and soil through its roots. This zone is a ‘hot-spot’ of microbial activity and trophic interactions with other soil organisms. It is here that growth of the plant root is influenced by nutrient availability, induction of root growth stimulating auxins, the interaction with plant pathogens and herbivores. Ecosystem engineers in the form of earthworms and other burrowing fauna are important in altering both the physical structure of soil and rates of decomposition of organic residues. A little researched component of soil is viruses. Their interaction with microbial and faunal communities is introduced here. Many of the soil processes influencing plant growth and the diversity of soil organisms is influenced by human activities ranging from agricultural and forestry practices through urbanization to the influence of pollution from industrial processes. To help us with the understanding of the interactions between biodiversity and function, new molecular tools involving metagenomics and transcriptomics are evolving, and are discussed here as an emerging suite of tools that can be applied to soil ecology. The chapter introduces the detail to come in subsequent chapters of this book.

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1.1 Introduction

Soil is fundamental as a medium for underpinning primary production in terrestrial ecosystems. Its development and fertility are dependent on a number of factors related to the origin of the mineral matrix, climate and nature of organic material returning to it from dead organisms. Soil is not just the physico-chemical constituents of the mineral and organic components, but is a living system with a vast array of microbes and animals interacting in both trophic and non-trophic ways to regulate the nutrient availability for primary producers. Biological interactions in soil are both competitive and synergistic and, because of the diversity and heterogeneity of resources supporting their growth, the diversity of soil organisms is probably second to none. Since many of the soil processes are dictated by a consortium of individuals from a wide variety of taxa, the health of a soil is very dependent upon the maintenance of this diversity and abundance of living organisms. This diversity can be modified significantly by human interactions especially in terms of modern agricultural and forestry practices, urbanization and consequent pollution. As such the aim of this book is to explore some of the more recent literature relating to the stresses imposed on soils in relation to the ability of soils to sustain plant growth in the face of pathogen attack and human influence (Coleman 2011).

Soil has been important to humans as both part of natural ecosystems and, especially, to underpin primary production of food and materials in the broad agricultural context. As inert structures the mineral component of soils has limited potential to provide all elements for plant growth. The recycling of old, dead organic matter by saprotrophs provides additional soil structure and nutrients mineralized from the organic matter. However, this organic material also brings into soil plant pathogens and the mere fact of having living plant parts (roots) in soil provides an entry point for plant pathogens. In a natural ecosystem it is suggested that the interaction between plants and their pathogens has evolved into a stable state of minimal effect of the pathogens (Harper 1990). In contrast, the modern agricultural ecosystem with a preponderance of monocrops, high fertilizer and pesticide use and the increased abundance of invasive plants and pathogens, tips the balance to favor the plant pathogen. Thus, to maintain a balance between soil organisms that are beneficial and detrimental to plant growth, it is strongly believed that the maintenance or development of a high diversity of soil organisms is desirable (Sylvan and Wall 2011; Bardgett 2005). Indeed this biodiversity has economic value as recently pointed out by Brussard et al. (2007) who priced the ecosystem services afforded by biotic diversity in soil has at around 760 billion US dollars worldwide. This consists of approximately \$90 billion year⁻¹ for N fixation, \$21 billion year⁻¹ for bio-remediation, \$160 billion year⁻¹ for biological pest control, \$180 billion year⁻¹ for useful products for humans and \$200 billion year⁻¹ for pollination services of insects with life cycles having a soil borne component. Given the importance of soil for sustainability of natural ecosystems and the agricultural production of food for the human populace for the last 10,000 years or so, why is it that understanding soil processes is still one of our frontiers of research (Coleman 2011)? Largely this is

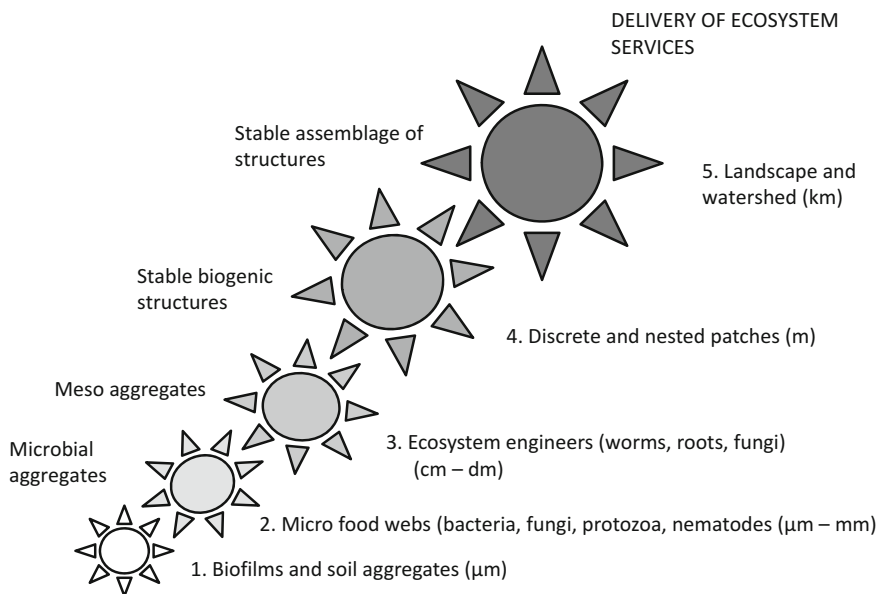


Fig. 1.1 Interactions between soil organisms at increasing scales of resolution to provide ecosystem services at the landscape level (After Lavelle et al. 2006 with permission)

because soil is an opaque medium of incredible physical, chemical and biological complexity with sophisticated self-organizing capabilities (Coleman 1985, 1998; Young and Crawford 2004; Crawford et al. 2005). Lavelle et al. (2006) suggested that these ecosystem services are emergent properties, manifest at the meter and landscape level by a series of small-scale functions that combine into large scale influences through a hierarchy of interlinking processes (Fig. 1.1). Ponge (2005) suggests that these emergent properties could be predicted from models of biological assemblages of which he discusses BUBBLES, WAVES and CRYSTALS. BUBBLES are structured entities constrained by an outer ‘envelope’ which imparts high resistance to the stable assemblage of organisms within, cites as soil aggregates. The similar structures CRYSTALS model consist of homogenous structures of discrete entities separated by attraction/repulsion forces, which maintains cohesiveness, in contrast to the envelope of the BUBBLE; he cites social animals such as ants and termites as examples. The WAVES model, in contrast is a dynamic model in a state of equilibrium imparting low resistance but high resilience to external forces, with examples such as patch dynamics and ecosystem surfaces. The use of such models in soil ecology is likely to enhance our understanding of the interactions and processes.

In the agricultural context (production of food or forest products), it is not just the nutrient supply provided by soil that is the only ecosystem service of importance. Soils harbor numerous pests (microbial and faunal) that reduce plant growth. ‘Suppressive soils’ are soils that have a good balance of organisms that include

many of those that are able to act as biocontrol agents against these pest species. The development and maintenance of suppressive soils for agriculture has led to discussions of best management practices and the adoption of no- or minimal-till agriculture in order to maintain soil biodiversity in monocropping systems (Kladivko 2001; Uphoff et al. 2006; Culman et al. 2010), where diversity has been reduced (Cluzeau et al. 2012; George et al. 2012). In this book we have attempted to bring together subject matter that is pertinent to discussion of the role of soil biodiversity to soil sustainability and the maintenance of suppressiveness or facilitation in a world where other human activities are imposing stresses on the soil ecosystem.

1.2 Suppressive Soils

Some 90 % of aboveground productivity is returned to the soil surface as dead organic matter (Gessner et al. 2010). The interactions between soil forming processes, dead organic matter and soil organisms results in decomposition and mineralization to release nutrients that support primary production. This process results from combined activities of diverse organisms living in the soil. In contrast to the supporting role of soil biota, a variety of organisms in soil can act as plant pathogens, reducing plant growth, productivity and fitness. Agricultural practices and, in particular, the widespread growth of monocultures of crop plants, generally results in reduced soil biodiversity and encourages the build-up of pathogens in soil (see Chap. 6 by Termorshuizen). To obviate this effect there is a large body of research into optimizing agricultural management techniques to encourage soil biodiversity and biodiversity that will suppress pathogens, leading to a disease suppressive soil. There are a number of examples where planting specific species leads to direct changes in soil biodiversity. For example Abawi and Widmer (2000) showed that incorporation of the cover crops sudangrass, rapeseed and ryegrass significantly reduced the severity of root knot nematode (*Pratylenchus penetrans*) on bean roots (*Phaseolus vulgaris*). In contrast, incorporation of alfalfa and hairy vetch residues into soil increases nematode abundance. Similarly Mazzola (2007) found that growing specific cultivars of wheat between rotations of apple tree plantations significantly increased the abundance of specific genotypes of fluorescent pseudomonads that suppressed the root rot fungus *Rhizoctonia solani*. These cases show that specific planting practices can increase the biodiversity of the soil by increasing more favorable organisms to offset the pathogens, and the converse is also true, that some plant species will increase the undesired species.

The return of organic matter into the soil not only augments that soil with nutrients (Parvage et al. 2013) and materials to promote better soil structure but can also add microbial communities that suppress plant pathogens (see review of microbial populations responsible for soil suppressiveness Weller et al. 2002). Research in composting methods have shown that microbial activity is enhanced during the composting process and that it is the microbial community within the compost that leads to greater disease suppression. In a meta-analysis, Bonanomi et al. (2010) showed

that microbial biomass, community composition and microbially induced processes are more important in disease suppression in composts than chemical attributes. Hydrolysis of Fluorescein diacetate (FDA) is one of the main indicators of suppressiveness (Schnürer and Rosswall 1982; Chen et al. 1988) along with population density of fluorescent pseudomonads and *Trichoderma* (Krause et al. 2001; Weller et al. 2002). Production of the antibiotic 2,4- DAPG (2,4-diacetylphloroglucinol) and PCA (phenazine-1-carboxylic acid) in soil is increased by the increased population of pseudomonad bacteria in the rhizosphere which inhibits take-all disease caused by the fungus *Gaeumannomyces graminis* (Weller et al. 2002). Similarly organic and integrated cropping systems increased both soil enzyme activity and rhizospheric bacterial communities to suppress aggressive weed species in Missouri corn agriculture (Kremer and Li 2003).

1.3 Soil Biodiversity

Why is it that soils support such a diversity of life? The diversity of resources of plant and animal remains decomposing in soil results in the distribution of soil organisms and their function at vastly ranging scales of resolution in both space and time (van der Putten et al. 2004). A particularly important temporal variation is that the physico-chemical characteristics of resources change during decomposition (Swift et al. 1979; Ponge 1990). Activities in soil at small spatial scales associated with aggregated distributions of microorganisms in relation to heterogeneity of physico-chemical soil structure can have effects at the landscape and ecosystem to global level (Young and Crawford 2004; Ettema and Wardle 2002). This heterogeneity in soil can be utilized differently by different groups of soil organisms (Nehr 2010) and may be the reason that greater biodiversity exists in soil than aquatic ecosystems (Gessner et al. 2010). Patches of resources in the soil can be considered as islands, whose colonization by microbial and faunal communities may be regulated by island biogeography theory (McArthur 1967). Similarly individual leaves have been considered as islands for colonization by phylloplane fungal and bacterial communities (Andrews et al. 1987; Hanski 1994). As Nehr (2010) points out, this has less frequently been explored for invertebrates, especially soil invertebrates, but see Rantalainen et al. (2004, 2005, 2006) and Åström and Bengtsson (2011), who showed colonization of new island resources by soil invertebrates at the scale of centimeters and Sarah Smith (unpublished MS Thesis, Rutgers University) at tens of meters.

The importance of interactions of biotic and abiotic components of soil at the micro-scale results in the formation of soil aggregates at about 20 μm diameter (Tisdall and Oades 1982). In aggregates that are stabilized by organic secretions from bacteria and fungi (Preston et al. 1999; Miller and Jastrow 1990) organic carbon can be sequestered and retained for periods of decades or more as Protected Organic Matter (POM), but can be readily lost by agricultural practices and land use change which causes physical breakdown of aggregates and consequent loss of C to the atmosphere with global consequences (Howard et al. 1995).

The regulation of soil processes are attributable to the complexity and diversity of plant litter chemistry, with top-down (predator effects on prey density and grazing pressure) and bottom-up (resource quality on microbial communities) processes occurring together. Sánchez-Moreno and Ferris (2007) show the importance of a complex soil food web in protecting agricultural food crops from pathogens (see trophic interactions Chap. 4 by Krumins). Complex and longer food chains containing omnivorous and predatory nematodes, as found in natural ecosystems, were better in suppressing plant-pathogenic populations than depauperate communities. One suggested mechanism is that predatory nematodes both increase soil ammonium N through grazing on microbivores, and increase suppressiveness significantly by decreasing the biomass of fungivorous, bacterivorous and plant pathogenic nematodes, lower in the food chain. In this way predatory nematodes either reduce diversity by eliminating some species or may be acting as a keystone species, reducing competitive exclusion and, thus permitting greater diversity.

Given that some 90 % of the 100 gigatons of global plant biomass is processed through soil systems (Gessner et al. 2010) there is a need to preserve the biodiversity of soil organisms to effectively recycle this material and make use of the nutrients contained within. However, it has been pointed out that there is a high level of functional redundancy in soil communities, so it is important to understand this in terms of spatial scale and heterogeneity and with respect to the responses of this community to perturbations (Wolters 2001). Thus, the development of suppressive soils is highly dependent upon the maintenance of soil biodiversity with appropriate functional attributes of a suite of beneficial organisms that can limit the detrimental aspects of plant pathogens (van der Putten et al. 2004). The impact of our agricultural practices, pollution and urbanization has placed considerable threats on soil biodiversity. Using a faunal index based on soil faunal community composition, Yan et al. (2012) showed a significant decrease in the faunal index (Fc) with increased land use in China. As a result, there has recently been a movement to propose legislative protection of soil biodiversity and ecosystem services provided by this diversity in the face of deleterious human activities. An example of such a measure in Switzerland in developing a Soil Monitoring Network (NABO) is highlighted by Havlicek (2012, see also Chap. 2) and is based on metrics of microbial biomass, soil respiration, mycorrhizal infection potential and earthworm populations, with the concept that biodiversity is the driving force of soil systems.

1.4 The Rhizosphere as a Unique Niche

The rhizosphere is a unique habitat within the soil at the interface of the plant root and the soil and is discussed in detail in Chap. 3 by Hol et al. Due to the leakage of carbohydrates and the sloughing off of dead root cells, the region is carbon and nutrient rich and thus supports unique communities of microbes. Microbial diversity is high in regions of available carbohydrates, especially in the rhizosphere. This carbon resource is important in sustaining a diverse and abundant microbial

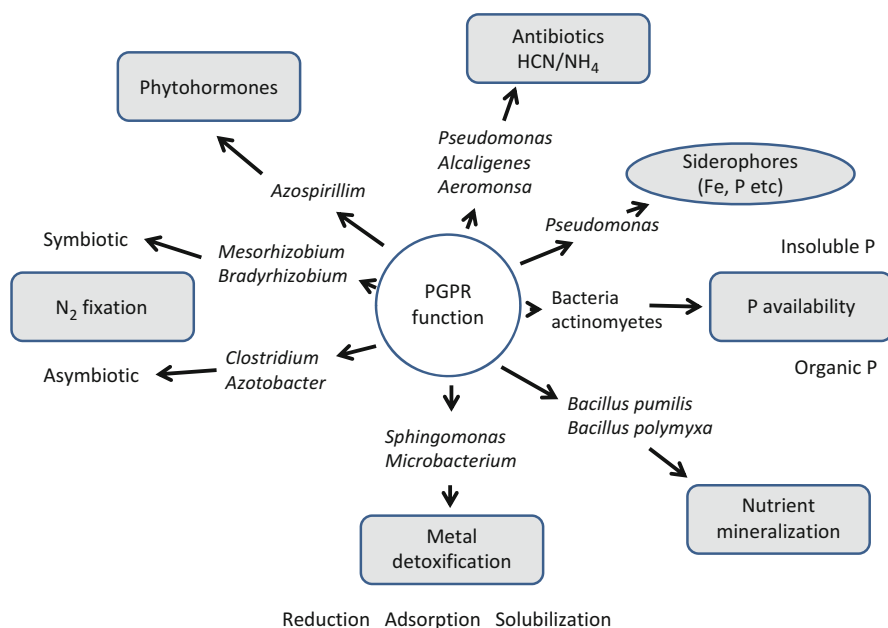


Fig. 1.2 Functional diversity among plant growth-promoting rhizobacteria (After Khan et al. 2009 with permission)

community and modifying soil moisture and hydraulic properties (Carminati and Vetterlein 2012). These microbes (bacteria and fungi) have important consequences for plant growth in terms of promoting nutrient mineralization through the ‘Microbial Loop’ (Clarholm 1994). In a review of the functional diversity of plant growth promoting rhizobacteria (PGPR), Khan et al. (2009) enumerated many beneficial functions derived from a variety of bacterial taxa (Fig. 1.2). In addition to the greater provision of nutrients via nitrogen fixation and phosphate solubilization, bacteria in the rhizosphere also produce phytohormones that regulate root growth and antibiotics and cyanide, which act as biocontrol agents against phytopathogens (Ahmazadeh and Tehrani 2009) and soil invertebrates (Devi et al. 2007). Additionally members of the PGPR can act as helper bacteria (*sensu* Garbaye 1994) and promote mycorrhizal development of roots by enhancing the recognition system between host and fungus. In their review, Hayat et al. (2010) list the benefits of rhizosphere bacterial communities as symbiotic N-fixation, non-symbiotic N-fixation, phosphorus solubilization, plant growth promotion by phytohormones and siderophore production.

Phyto- and micro-siderophores are exuded, small, metal-binding molecules that are particularly important in complexing Fe to enhance its uptake by plants, particularly when these metal ions are in low abundance (Hartmann et al. 2009). This siderophore Fe complexing aids in P mobilization by transforming hardly soluble PO₄ to soluble PO₄ in acidic soils (Whitelaw et al. 1999; Marschner et al. 2011). Iron uptake

from micro-siderophores of *Streptomyces* is enhanced by the presence of other heavy metals such as Al, Cu, Mn, Ni and U (Dimka et al. 2009), although it has been shown that at low siderophore abundance there is competition for binding sites between Fe and Mn, where Mn can displace Fe (Duckworth et al. 2009).

Predation in the rhizosphere can also be beneficial to plant growth where grazing targets root grazing animals or soil dwelling life stages of aboveground herbivores. Entomopathogenic nematode populations and species can be regulated to optimize reduction of root feeding grubs (Preisser 2003; Ebssa and Koppenhöfer 2012; Ebssa et al. 2012) which may be facilitated by plant volatiles released in response to insect herbivory (Ali et al. 2012). Free-living predatory soil mites can have a significant impact on the population densities of soil dwelling pupal stages of leaf feeding thrips (Navarro-Campos et al. 2012). They showed that the higher abundance of the predatory mite *Hypoaspis aculeifer* was correlated with lower abundance of Kelly's citrus thrip (*Pezothrips kellyanus*). Addition of manure to soil increased the abundance of predatory mites, suggesting that there are positive management action that can enhance this interaction.

1.4.1 Anti-fungal Properties of the Rhizosphere

The rhizosphere microbial community is important in controlling pathogenesis and root grazing (see Chap. 3 by Hol et al.). Ahmadzadeh and Tehrani (2009) identified 42 isolates of fluorescent *Pseudomonas* spp. which were antagonistic to the root fungal pathogen *Rhizoctonia solani* and 21 isolates antagonistic to *Pythium ultimum*. All but two isolates had plant growth promoting attributes, but different isolates imparted this function to different parts of the host plant (stem length, root length, leaf number or root number). Similarly, Yuttavanichakul et al. (2012) inoculated roots of peanut with PGPR and inhibited the seed borne pathogen *Aspergillus niger*. The *Bradyrhizobium* spp. and *Pseudomonas fluorescens* isolates used showed an average of 40 % reduction in fungal pathogenicity. The importance of the legacy of the rhizosphere in maintaining suppressiveness in commercial nursery conditions has been shown by the work of Clematis et al. (2009). They showed increased suppressiveness against *Fusarium oxysporum* in recycled and non-autoclaved soilless potting mixes, where rhizobacteria were retained, compared to new potting media; possibly altering ideas of management practices in horticulture. Indeed the manufacture of good compost and careful brewing of compost teas can provide a beneficial mix of microorganisms and fauna that promote defense against root and foliar pathogens as well as enhanced nutrient availability for plant growth (Ingham 2005; de Bertoldi 2010).

PGPR and plant defense microorganisms do not work independently or in isolation, but rather as part of a community of mixed functional groups. To investigate possible synergistic interactions between these two functional groups, Felici et al. (2008) applied the biocontrol bacterium *Bacillus subtilis* and the PGPR *Azospirillum brasiliense* alone and in combination on tomato roots to identify

possible synergism. However, no synergism was found and any benefit imparted by either bacterium was lost in co-application. They suggested that each bacterium species responded differently to signaling cues in the plant/bacterial interaction and that these signal may become mixed in a dual inoculums situation. However, induction of plant defense chemistry by rhizospheric bacteria has been shown by Sundramoorthy et al. (2012) who used a combination of an endophytic bacterium (*Bacillus subtilis*) and rhizospheric PGPR bacterium (*Pseudomonas fluorescens*) against the root pathogenic fungus, *Fusarium solani* in chili plants. They showed that the combination was synergistic in promoting induced systemic resistance (ISR) as determined by enhanced production of peroxidase (PO), polyphenol oxidase (PPO), phenylalanine ammonium-lyase (PAL) and chitinase activity and increased phenolic compounds levels in the plant. Further studies will elucidate if these interactions are more common than we understand them to date, and additionally we need to know more about these chemical and molecular signaling systems in the assembly of rhizosphere microbial communities. A review of the influence of plants on the selection of rhizosphere microorganism community is given by Hartmann et al. (2009). They distinguish between stimulatory factors (carbon exudates, vitamins etc.) inhibitory factors (volatile and soluble antimicrobial chemicals and quorum sensing inhibitors), stimulatory feedbacks (solubilization of nutrients, growth regulators, pathogen resistance) and inhibitory feedbacks (competition for nutrients and phytotoxic and allelochemicals) (see Chap. 7 by Pavlovic et al.). Since most plant species are frequently also associated with symbiotic mycorrhizal fungi, the signaling system can become very complex and warrants further investigation. The association between PGPRs and mycorrhizae has only recently attracted attention, where the concept of the 'Helper Bacteria' goes beyond assistance with the recognition system between fungus and its host plant, to establish the symbiosis, to a plant growth enhancement in a tripartite association (Hryniewicz et al. 2010).

There is potential for engineering rhizosphere microbial communities and traits of members within that community to benefit plant growth and crop production. Some of these ideas are discussed in the review by Ryan et al. (2009).

1.4.2 Herbivory Protection in the Rhizosphere

Rhizobacteria capable of producing toxic secondary metabolites are also important in protecting roots from herbivory. The production of hydrogen cyanide by rhizobacteria was shown to have significant effects in reducing root grazing by termites in *in vitro* experiments (Devi et al. 2007).

Fungi are also important in protecting plants from herbivory. Singh et al. (2012) suggested that rhizospheres could be enhanced with nematode trapping fungi to reduce root nematode populations. In vitro studies of the nematode trapping fungus *Arthrobotrys oligospora* against the nematode *Meloidogyne graminicola* showed a high efficiency of trapping in some fungal isolates. A dual plant protective role was also established as *A. oligospora* significantly reduced lesion formation by the plant

pathogenic fungus *Rhizoctonia solani* by approximately 50 %. Synergistic interactions between various nematode trapping fungi and the nematode egg parasitizing fungi of the *Trichoderma* genus were found *in vitro* by Szabó et al. (2012). Recently the concept of signaling information about herbivore attacks between plants via mycorrhizae has been suggested (Babikova et al. 2013). Volatiles produced by aphid infested bean plants (*Vicia faba*) can be passed from infested plants to un-infested plants where they invoke herbivore defenses. However it was shown that this effect occurred only if plants were mycorrhizal. Infested plants transferred a mycorrhizal signal to un-infested plants to produce volatiles that repelled aphids, but attracted aphid parasitoids and this signal was lost if mycorrhizal hyphal connections were broken.

The possibility of introducing a biocontrol agent directly to soil, to defend a plant against aboveground herbivory, is an appealing concept which may overcome the potential loss of the active agent during aerial application. Brownbridge et al. (2012) compared seed or root application of the endophytic fungus *Beauveria bassiana* to pines to control for bark beetles. However only one plant showed positive for retaining *B. bassiana*, so soil delivery is probably not possible.

1.4.3 *Mycorrhizae as a Component of the Rhizosphere*

We have been investigating the diversity and function of mycorrhizae for over 100 years, developing knowledge of their ecosystem function of supporting primary production by nutrient and water acquisition along with their role of defending plant roots from pathogens and herbivory. There are many good descriptions of mycorrhizae and their role in the ecosystem (Smith and Read 2008; Dighton 2009a, b). Their role in agriculture to promote plant growth and crop yield has been discussed in relation to farming intensity (Plenchette et al. 2005; Gosling et al. 2006) who highlight the points that high intensity agriculture reduces arbuscular mycorrhizal activity, which is compensated for by the application of fertilizers and pesticides. Both papers provide evidence for improved AMF activity and function in organic and minimal till agriculture, avoiding the need for exogenous chemical inputs. Indeed it has been suggested and demonstrated that cultivation of arbuscular mycorrhizal propagules for inoculation into agriculture is economically viable (Estaún et al. 2002; Douds et al. 2010) however, Plenchette et al. (2005) make a case for encouraging indigenous mycorrhizal communities as the efficacy of selected AMF strains is often lower than native strains. These methods may produce a local and more diverse mycorrhizal community for inoculation than inocula developed on single host species (Hetrick and Bloom 1986).

Mycorrhizae do not work alone and a number of studies have shown synergistic interaction between mycorrhizal fungi and bacteria. Bianciotto et al. (2002) mention the endosymbiotic bacteria of arbuscular mycorrhizae, such as *Burkholderia*, that show gene expression that stimulates phosphate transporter systems. Garbaye (1994) also identified the interaction between fluorescent pseudomonas and

ectomycorrhizae having a role in helping the initiation of the fungal-root association to form a mycorrhizae; termed 'helper bacteria'. More recent investigations of these multitrophic complexes (Frey-Klett and Garbaye 2005; Frey-Klett et al. 2005; Schrey et al. 2005) have shown that these interactions increase the plant's ability to defend itself from fungal pathogens, and upregulate genes associated with root growth, hyphal growth (e.g. protein kinase), inorganic P solubilization and siderophore production. This is an area of research that is little understood and may be important in selecting mycorrhizal and bacterial strains for inoculation to improve crop production.

To a certain degree, plants are able to defend themselves against pathogens with a cascade of signaling processes leading to the upregulation of genes selecting for the production of plant defense chemicals such as reactive oxygen species (ROS) and pathogenesis-related (PR) proteins (Pozo et al. 2002). Many of these genes exist in arbuscular mycorrhizal fungi which enhance the potential induction of disease defense. Additionally, Azcon- Aguilar et al. (2002) point out that benefits of the mycorrhizal symbiosis help the plant in its defense against pathogens by improved plant nutrition to compensate for damage, favoring competition between the mycorrhiza and pathogen for plant derived carbon, creating physical changes to root architecture and enhancing PGPR bacteria abundance. Genetic control of the establishment of mycorrhizal associations and regulation of pathogen defense are also being identified. Anderson et al. (2010) showed that both the Nod factor, introduced into roots by Rhizobia, and the Myc factor, introduced by mycorrhizal fungi leads to a calcium signaling system that causes the root to accept the appropriate symbiotic association. Once accepted, the arbuscular mycorrhiza can upregulate genes to enhance the host plant defense against root pathogens, along with other genes that express pathogen defense in leaves (Campos-Seriano et al. 2012).

The ecological implications of mycorrhizal associations in plant interactions has led to a more synecological approach to the interactions between these fungi, their host plants, soil fauna and microflora with respect to competition and plant survival (Pedersen and Sylvia 1996). The concept of the mycelial network, where plants are connected to a common mycorrhizal community in natural ecosystems, allows both the transfer of nutrients and carbon between plants (Newman 1988; Newman et al. 1992; Simard et al. 1997a, b, Read etc.). An additional benefit has been shown that these networks can carry information as warning signals between interconnected plants inducing herbivore defense in recipient plants from signals provided from a herbivore damaged donor plant (Babikova et al. 2013). Periodic disturbance of the mycelial network in agricultural soils due to tillage practices both reduces the opportunity of mycorrhizal colonization of roots by mycorrhizal fungi, but also limits these potential beneficial effects of sharing resources and information between plants.

Pathogen defense in ectomycorrhizal roots (Machón et al. 2006; Itoo and Reshi 2013) may also have genetic control of host defense systems, but has also been shown to present a physical barrier to pathogens afforded by the mantle (sheath) and Hartig net (Branzanti et al. 1999). The generation of disease resistance chemicals is not only enhanced within the root system of ectomycorrhizal plants, but can be

expressed in leaves. Pfabel et al. (2012) have shown mycorrhizal induced changes in the condensed tannin to total phenolics ratio in leaves and the maintenance of high levels of fungal antagonistic flavenoids and lipids in poplar leaves in relation to rust attack.

The combination of physical and genetic control of plant pathogens by mycorrhizae is a relatively new area of study. With the development of more sophisticated transcriptomic and genomic tools (see below) this is an area of research that will lead to much greater understanding of this aspect of mycorrhizal physiology.

1.5 Viruses

Viruses are well known disease agents of plants that can be introduced to plant roots by soil faunal vectors such as nematodes (Verchot-Lubicz 2003) for tobacco rattle virus or protozoa (Kanyuka et al. 2003) for rosette disease of cereal. However Coleman (2011) points out that little attention has been given to viruses in soil, despite the understanding that a small but significant amount of C is cycled through viral components in pelagic ecosystems. Small spherical viruses form the major portion of the morphological classes of virus in soil under wheat cultivation (Swanson et al. 2011) and it is interesting that they show no difference in viral abundance between rhizosheath, rhizosphere and bulk soil despite a significant reduction in bacterial numbers in bulk soil compared to the rhizosphere. This suggests that many viruses in soil are not directly associated with bacterial hosts. In their metagenomic analysis of bacteria, archaea, fungi and viruses in soil, Fierer et al. (2011) showed a large diversity of viruses with less similarity in community composition between ecosystems than archaea and fungi, although soil communities clustered closer together than those from other environments in a similarity analysis. A greater discussion of the role of viruses in soil is provided in Chap. 8 by Reavy et al.

A full understanding of interactions between components of the soil biota probably requires metadata analyses to determine patterns in the ecosystem from the micro-scale in soil to the landscape level (Gessner et al. 2010). From a microbial perspective, Young and Crawford (2004) caution that in order to understand the complex interactions occurring at varying physical scales and across different time scales in soil still presents a major challenge that will require microbiologists, molecular biologists, soil physicists and theoreticians to work closely together. The use of new tools to examine genetic regulation of enzyme activity such as proteomics and transcriptomics has promise to elucidate fine-scale microbial activity (van Elsas et al. 2008) and will be useful in the aim of scaling up from the genome to ecosystem level processes (Eijsackers 2001). New methods are also being developed to investigate the effects of microorganisms on the physical and chemical changes in their resources at the scale of resolution at which the interactions occur. A combination of microscopic ATR-FT-IR spectroscopy and atomic force microscopy has been applied to the understanding of the physical and chemical processes occurring at the individual fungal hyphum/resource interface (Oberle- Kilic et al. 2013).

1.6 Earthworms: Ecosystem Engineers and Soil Disturbance

Plant growth is not just dependent on the fertility of soil, but also on water availability and synergistic interactions of soil organisms at a larger scale. Local soil perturbations by larger invertebrates in soil have effects on both the chemical and physical structure of soil. The role of earthworms in bioturbation was first suggested by Darwin (1881 cited in Meysman et al. 2006) and has subsequently led to the use of the term ‘ecosystem engineers’ (Jones et al. 1994) for the activity of organisms such as these. Meysman et al. (2006) suggest that the burrowing habit has been an important evolutionary development in invertebrate animals and the effects of the burrowing activity of earthworms has major consequences on soil properties by creating a porous matrix of solid particles that are coated with organic polymeric secretions of the worms. Lavelle et al. (2006) stresses importance of earthworms as ecosystem engineers (also ants and termites in dry systems) for physical, chemical (casts, plant hormones, allelopaths) and biological (soil fauna) effects, altering plant assemblages, seed dispersal etc.

Scheu (1987a) described the burrows and casts formed by earthworms in forested ecosystems, which has been followed by descriptions of soil profiles worked by earthworms where their burrows, casts and influences on soil aggregates provide defined soil characteristics that affect soil porosity, drainage and soil stability (Piron et al. 2012). As a result of bioturbation, organic matter is brought into the soil matrix by earthworms. In post-mining reforestation Frouz et al. (2009) found that carbon accumulation was positively correlated with earthworm density. The chemical nature of this carbon may also be altered in the presence of earthworms, where *Lumbricus rubellus* activity significantly changed the aliphatic and aromatic composition of particulate organic matter in mid-succession NE American forest soils, resulting in changes in C stability in these soils (Crow et al. 2009). The influence of earthworm activity can be seen particularly in the north east US where earthworm invasions have significantly altered landscapes (Bohlen et al. 2004a, b). In a relatively undisturbed forest soil, earthworms reduce soil C by 28 % and enhanced nitrate leaching. The increase in availability of N for leaching is likely to be an enhancement of the mineralization processes effected by the microbial community. N mineralization is positively correlated with earthworm abundance (Scheu 1987b) and may be induced by the priming effect of earthworm secretions on the microbial community (Bityutskii et al. 2012), although the increase in microbial biomass induced by earthworms was only seen in mineral soil, not the surface organic horizons by Groffman et al. (2004). Here, worm incorporation of organic matter into mineral horizons was correlated with increased soil respiration, organic matter mineralization and production of higher concentrations of labile nitrogen. Similarly, increase in the production of labile P in the mineral soil and its increased rate of leaching was also attributed to earthworm activity (Suárez et al. 2004). Much of this increased P availability can occur in earthworm casts on the soil surface or within the soil matrix (LeBayon and Binet 2006). Although much information has been gained on the physico- chemical changes of soil attributed to earthworms it is still difficult to scale

up the effects of earthworms in relation to the feedbacks to worm populations and other environmental metrics by the changes that worms effect. Schneider and Schröder (2012) suggest there are three main challenges hindering the development of robust models. These are (i) the inability to reliably and adequately link processes to earthworm populations across scales, (ii) to use information gained from different earthworm species to combine in an appropriate mixed species model, and (iii) obtain adequate metrics for soil porosity and water flow etc.

Earthworms can directly and indirectly influence plant growth and plant community composition. Kreuzer et al. (2004) investigated the effects of collembola and earthworms on the growth of *Lolium perenne* and *Trifolium repens* where contrasting effects occurred depending on animal species. Earthworms or collembola alone did not increase N uptake in either plant, but when combined their actions were synergistic and increased biomass in both plant species. The effect of collembola was to increase biomass of *T. repens*, but decrease that of *L. perenne*. Loranger-Merciris et al. (2012) showed that the earthworm *Pontoscolex corethrurus* reduced the abundance of root parasitic nematode *Pratylenchus* spp. by 50 % in banana crop soil. This they attribute to the bioturbation increasing microbial activity that are detrimental to the nematode and the fact that the increase in abundance of 3–300 µm diameter pores in the soil may disrupt nematode movement and survival.

At a larger scale of resolution, pocket gophers have been shown to move soil up to 40 cm upslope to their burrows (Cox and Allen 1987) and vizcaca (*Lagostomus maximus*) activity significantly increases plant growth and nutrient content around their burrows by increasing N and P availability and bring up large quantities of caliche (calcium carbonate sedimentary rock) from depth, which significantly increases P availability in surface soils (Villarreal et al. 2008). Indeed Gutiérrez and Jones (2006) cite a number of major activities carried out by ecosystem engineers that influence physical and biochemical process. However, the activities of these larger soil bioturbators is usually more local in focus than that of earthworms.

1.7 Pollution, Urbanization and Invasive Species

As we can see by Hazelton and Clement's chapter on urban soils (Chap. 10), the changes imparted to soils due to urbanization are large and consist of compaction, pollution and alteration of vegetation. As a result, soil biodiversity is reduced along with the function. However, even in the face of these stressors life persists in these soils and the functions of a number of organisms are able to remediate these soils. In contrast to the measurement of pollutant concentration in soil, the use of bioindicators to assess the degree to which a soil has been impacted is probably more informative (van Straalen and Løkke 1997). However these measures are dependent on a suitable suite of bioindicators that are both realistic and appropriate for the soil type under consideration. For example there has been a large body of information on the use of ectomycorrhizal fungi as bioindicators of acid rain and N-deposition (Jansen and Dighton 1990; Dighton and Jansen 1991;

Termorshuizen and Schaffers 1987; Lilleskov et al. 2002; Dighton et al. 2004), where pollution has resulted in changes in ectomycorrhizal community composition. The impact of chronic N deposition appears to be stronger than short term acute deposition where immediate trends in response appear to be larger in the bacterial community than the mycorrhizal fungal community (Krumins et al. 2009). Across a European gradient of N deposition Zechmeister-Boltenstern et al. (2011) showed that despite an increase in bacterial stress markers (cyclopropyl fatty acids) the bacterial to fungal ratio in soil increased with increasing N-deposition. What is missing, to a large degree, is the translation of community change resulting from pollution into the functional changes that are occurring at the local and landscape level. It is likely that the evolution of biotic interactions in soil are linked to changes in stoichiometry of available nutrients (Kay et al. 2005), but the functional aspect is likely to be revealed using molecular techniques as described below.

From an understanding of the impact of pollutants on components of the soil biota, we can investigate how these soil organisms are involved in alleviating the effects of pollutants and could be managed for restoration. It is known that both bacterial and fungi are important in degrading pollutant chemicals (Radwan 2008), with basidiomycete fungi and bacteria having the ability to degrade polyphenolics (Gadd 2004; Cravotto et al. 2008), with some fungi being able to use volatile aromatic hydrocarbons as their sole energy source (Prenafeta-Boldú et al. 2001a, b), however the presence of ectomycorrhizae appears to suppress the decomposition of PAHs (Joner et al. 2006). Mycorrhizal fungi are important players in the rhizosphere enabling both heavy metals (Sessitsch and Puschenreiter 2008) and radionuclides to be retained in the fungal structure and limiting uptake into plants and the fruit bodies of ectomycorrhizal species have been shown to be hyperaccumulators of both metals and radionuclides (see reviews by Leyval et al. 2002; Dighton 2009a, b; Dighton et al. 2008). It has been proposed that this functional group of fungi could be used for bioremediation of heavy metal and radionuclide polluted sites by removal of fungal fruit bodies from contaminated sites (Gray 1998; Leyval et al. 2002; Turneau and Haselwandter 2002).

Polluted and urban sites are frequently altered in their physical structure, especially when related to industrial sites. Soil compaction is an important change that also occurs under intensive agriculture. It has been pointed out above that earthworms are important in changing the physical properties of soil. In an urban restoration context, the introduction of earthworms into the soil community is an important aspect of alleviating soil compaction and reducing lateral flow of water etc. (Yvan et al. 2012; Guéi et al. 2012). The development of a diverse and complete soil biota is, therefore, an important aspect to the success of restoration of soil physical structure and functionality in nutrient cycling.

With the increased traffic in people and materials around the world many organisms either intentionally or inadvertently get transported to areas where they are not native. For some of these organisms it provides an escape from natural predators and pathogens and the species becomes an invasive in its new habitat. In Chap. 9, Elgersma discusses the feedback effects that occur between invasive plants and soils that influence the success of the invasive in competition with the native vegetation

and that the changes in soil conditions arising may support the invasive species (Ehrenfeld 2003). The role of mycorrhizal associations may either enhance the invasive potential of a plant or, by the lack of appropriate mycorrhizal species, reduce the spread of an invasive plant or a plant of economic value that is being grown in a new area (e.g. exotic tree species such as pines in S. Africa and Eucalypts in S. America (Richardson et al. 2000)). These invasives are not restricted to plants and the introduction of exotic plant pathogens can alter the plant community in such an extensive way that plant litter inputs to the soil change considerably (Appiha et al. 2004; Wingfield et al. 2001).

Even without invasive species or pollution, a lot of what humans do to ecosystems by altering the landscape and its vegetation for agriculture, forestry and management of natural ecosystems in the name of conservation can have a profound, and usually negative, effect on soil biodiversity (Adl et al. 2006; Cluzeau et al. 2012). In managed forest ecosystems the increased demand on the use of post-harvest residues is likely to cause significant decreases in soil biodiversity, soil fertility and stability (Helmisaari et al. 2011; Merilä et al. 2013). Many of the factors negatively influencing soil biodiversity are discussed in Chap. 5 by Pérès.

1.8 New Tools in the Tool Box: Molecular Determination of Diversity and Transcriptomics for Function

With reduced costs and more rapid screening methods, molecular analysis of community composition of components of ecosystems is becoming a much more common technique. Lombard et al. (2011) states that ‘soil represents an as yet almost untapped genetic reservoir, which has just started to reveal its secrets.’ Microbial community composition is being assessed by DNA extraction and subsequent PCR amplifications followed by denatured gradient gel electrophoresis (DDGE), terminal restriction fragment length polymorphism (T-RFLP), single- strand conformational polymorphism (SSCP) and ribosomal internal spacer analysis (RISA) along with gene sequencing to identify individual species. These methods have been widely applied to bacteria and fungi, but less so to other groups of organisms with important functional roles in soil. In a comparison between a beech (*Fagus sylvatica*) and spruce (*Picea abies*) forest soil, Damon et al. (2012) extracted DNA and mRNA from soil micro- and meso-fauna to determine molecular diversity. More than 50 % of the DNA had no match to current databases, suggesting that our knowledge base is severely lacking for these groups of soil organisms. Molecular methods are not without sampling and interpretation problems. Lombard et al. (2011) caution that there are methodological problems associated with adequate sampling (replication) from a complex and heterogeneous medium and quality control of the molecular method to optimize DNA extraction.

Not only can the identity of organisms be revealed using molecular techniques, but the functional traits of an organism and/or its response to environmental variables can be measures in terms of gene expression or transcriptomics; an emerging field

in soil ecology. In their review of microbial interactions in the development of suppressive soils, Weller et al. (2002) identified a number of future areas of microbial genetics which would help elucidate the characterization of the effective microbial players and their mechanism of action. Some of these ideas have been taken up by van Elsas et al. (2008) in their METACONTROL project. Using new methods of metagenomic analysis and transcriptomics combined with sequencing analysis it will be possible to obtain data to correlate the diversity of the rhizosphere microbiology with function (Yadav et al. 2010; van Elsas and Boersma 2011). Gene mapping of the basidiomycete fungal root biotroph *Piriformospora indica* has revealed its intermediary position between saprotroph and obligate biotroph (endophyte) as it lacks some genes for nitrogen metabolism (biotrophic trait) but has a large array of enzyme activities akin to a saprotroph (Zuccaro et al. 2011). These approaches have a lot to offer to the future understanding of microbial functionality in soil.

Assessment of functionality comes from clone libraries and sequencing, linked to functional genes, but it needs a large sample to adequately sample the whole microbial community and avoid a bias of information from common or abundant species. Functionality can be assessed through DNA Microarrays which match gene coding DNA to similar products in soil or through pyrosequencing which identifies coding for specific known enzyme functions within the microbial community. Also the use of transcriptomics identifies transcriptional mRNA in soil to assess gene function. However, it is probably also important to look not only at the transcript level (Kellner et al. 2010), but also at the post-transcriptional level, to observe real time gene expression. Looking at enzyme activity in different ways allows us to understand what processes are occurring without the need to identify specific species in the complex microbial community in soil.

Brulle et al. (2010) review the progress of transcriptomics as applied to soil fauna. They concentrate largely on measures of gene expression in response to metals and PAHs (polyaromatic hydrocarbons) as pollutants. For example they cite that some 290 genes have been identified to be expressed in nematodes in response to Cd exposure, of which only about 30 % can be assigned to a known function. LumbriBASE (a data base of expressed sequence tags) has been used to develop microarrays for detection of earthworm responses to heavy metals. It could be foreseen that these methods could replace existing ecotoxicological methods as bioassays of soil health. Genetic adaptation is not restricted to soft-bodied fauna, as tolerance to Cd in the collembolan *Orchesella cincta* is reported to be due to inherited enhancement of Cd excretion by the upregulation of a single-copy gene (Brulle et al. 2010). Nota et al. (2009) used microarrays to determine the effects of PAH's on transcripts related to detoxification and biotransformation enzymes in the collembolan *Folsomia candida*, and up-regulation of heat shock proteins in response to temperature (Nota et al. 2010). In both cases they propose new rapid and sensitive soil toxicity tests.

The utility of these methods is derived from the study of model organisms in putative functional groups of microbes. The use of gene knock-outs in combination with transcriptomics could provide a transition from model organisms into the 'real world' system (Lee and Dighton 2013). However, Nehr (2010) has shown that

molecular primers developed for the model nematode *Caenorhabditis elegans* do not work with a number of groups of soil dwelling bacterivorous nematodes, so the translation of information from model organisms to similar groups in the natural world may not be as simple as thought.

1.9 Conclusion

Soil is a complex milieu of physical and biological entities that regulates the availability of nutrients for plant growth. The interactions between the elements of the soil biota and the plants during this process are complex and often rely on feedbacks between the plants and the soil organisms, either by trophic interactions (Krumins Chap. 4), or direct interactions between plants and plants or plants and microbes via allelopathy (Pavlović et al. Chap. 7). The diversity of soil organisms is critical to maintain the functions and ecosystem services of soil and in systems where diversity had been reduced, methods of remediation are being investigated (Havlicek and Mitchell, Chap. 2). The close association of this soil diversity and the plants which are supported by the soil fertility come together around the root. This rhizosphere and its mycorrhizal component are important parts of the connection between the plant and soil through its roots. This zone is a 'hot-spot' of microbial activity and trophic interactions with other soil organisms. It is here that growth of the plant root is influenced by nutrient availability, induction of root growth stimulating auxins, the interaction with plant pathogens and herbivores (Hol et al. Chap. 3). It is in the rhizosphere that plant roots encounter pathogenic organisms (Termorshuizen Chap. 6), against which the maintenance of or development of a suppressive soil is so important for our crop plants. Ecosystem engineers in form of earthworms and other burrowing fauna are important in altering both the physical structure of soil and rates of decomposition of organic residues. A little researched component of soil is viruses. They are known as plant and animal pathogens, but their interaction with microbial and faunal communities is multifaceted, which leads to question of evolution of many microbial groups by horizontal gene flow and lysogeny (Reavy et al. Chap. 8). Many of the soil processes influencing plant growth and the diversity of soil organisms is influenced by human activities ranging from agricultural and forestry practices (Pérès, Chap. 5) through urbanization to the influence of pollution from industrial processes (Hazelton and Clements, Chap. 10). Increased travel between continents leads to inadvertent or intentional movement of plants and their associated pathogens from one continent to another. Some of these plant species are opportunists that find a vacant niche and flourish as invasives. These niches can become available if soil biodiversity is low or if soil management creates more suitable conditions for the exotic plant than natives. Once established it is possible for these invasive plants to alter soil condition to increase their competitiveness and survival (Elgersma, Chap. 9). To help us with the understanding of the interactions between biodiversity and function, new molecular tools involving metagenomics and transcriptomics are evolving, and emerging as a suite of tools that can be applied to soil ecology.

However, it is only by combining all facets of our knowledge of soil ecology that we can approach the understanding of how soils, soil biodiversity and the interactions within that diversity that we can approach the science in a holistic way (Coleman et al., Chap. 11). Soils underpin primary production in all terrestrial ecosystems. Soils may take centuries to form and can be damaged and destroyed readily by mis-management. As the human race makes increasingly greater demands on the soil reserves we have, it is our responsibility to conserve and maintain soils in such a way as to ensure continued plant growth in both managed and natural ecosystems.

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Chapter 2

Soils Supporting Biodiversity

Elena Havlicek and Edward A.D. Mitchell

Abstract Soils are complex systems. Soil organisms and mineral components interact to generate high diversity and complexity, feeding back to biodiversity through habitat provision. Vascular plants link the aboveground and belowground components of ecosystems by litter inputs, root exudates, and influence soil chemistry and structure. Soil mineral composition and soil organisms together determine soil characteristics and fertility. Soils organisms differing in size and function create soil structure and aggregates, which are hotspots of microbiological diversity and activity. Soil structure is thus both a product and a cause of soil biodiversity.

Soil structure degradation leads to compaction, which decreases transfers of fluids and nutrients. An adequate input of organic matter is necessary to maintain soil fertility by enhancing aggregate stability and organic matter input is therefore an easy measure to improve soil fertility.

Soil use affects above and belowground biodiversity through cascading effects across all spatial scales. However soil biodiversity is generally not considered in land-use planning and the vast majority of soil organisms are unknown.

Long-term ecological studies and recent advances in molecular methods provide huge potential for assessing the relationship between soil taxonomic and functional diversity and ecosystem function and the consequences of biodiversity loss and changes in community structure.

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Given its functional importance, soil biodiversity clearly deserves more attention in education programs, improved knowledge transfer and more resources for fundamental and applied research.

Unsustainable use of soil is partly psychosocial in nature, stemming from diverse representations of the environment. Sociological approaches should be given more attention to improve the successful implementation of knowledge into sustainable soil management.

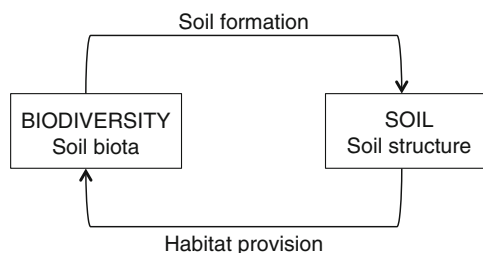
2.1 Introduction

Ecosystems are truly complex systems. This is especially true for the soil compartment of terrestrial ecosystems and this complexity is the key to their role in supporting biodiversity. In this chapter we will address some of the main aspects of soil complexity with special reference to the way it influences biodiversity and ecosystem function. We will particularly focus on soil structure as it is at the same time the product of biological activity and, through feedback effects, the main driver of soil biodiversity.

Biodiversity, which has been a very popular concept for over two decades amongst both scientist and the larger public, is mainly used as a tool to measure the state or the quality of a given ecosystem. This is intuitively based on the assumption that ecosystems are more valuable if their species count is higher. This view however fails to acknowledge the value of naturally species-poor ecosystems such as Northern *Sphagnum*-dominated peatlands, which are of global significance for C cycling and regionally of high value for biodiversity conservation (e.g. in Switzerland where they do not naturally account for a high proportion of the landscape). The basic concept of biodiversity does not either account for functional biodiversity, i.e. the diversity of ecosystem functions or how species contribute to them. For instance, species diversity can be very high in urban ecosystems, often substantially higher than in adjacent agricultural landscapes (e.g. Savard et al. 2000; Alvey 2006; McKinney 2008). However this high diversity is primarily due to the presence of exotic species (Faeth et al. 2011), which do not necessarily play important ecological roles in the communities. Furthermore many of these species would not be able to maintain viable populations naturally while others behave invasively and constitute a threat to biodiversity and/or to human health. Research is therefore increasingly focusing on how biodiversity relates to ecosystem function.

Biodiversity loss is of increasing concern at both scientific and policy levels (Mace et al. 2005). However the link between biodiversity and ecosystem function – and hence the degree to which its loss should be a matter of broader concern – although now relatively well studied for the above-ground compartment of terrestrial ecosystems (Hooper et al. 2005) remains less well understood in soils (Decaëns 2010). For instance, a forest in the narrow sense of the term should be described as a community of living organisms, plants, animals and microorganisms that can – theoretically – be quantified (e.g. species number) and qualified (e.g. interactions among species

Fig. 2.1 The soil functional loop



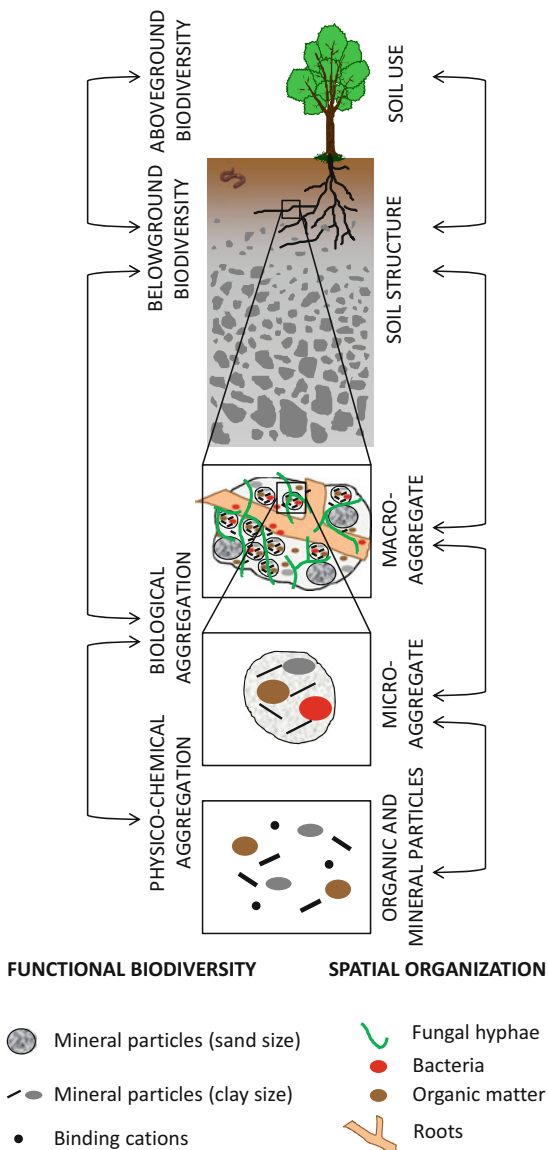
and between species and their environment). The presence and interactions of forest organisms depend on external environmental factors such as climate, geology or topography. In contrast to the forest example, soils represent more than only a spatial portion of an ecosystem harbouring adapted species; they are ecological systems in which the living organisms are inextricably and functionally intertwined with inorganic components (Fig. 2.1). This tight connection enhances their diversity (both taxonomic diversity and diversity of soil types) and structural and functional complexity. Soil biodiversity also stems from the tiny size of organisms relative to the spatial scale of the aboveground part of terrestrial ecosystems and the arrays of functions involved in decomposition mechanisms, which are almost uniquely performed in soils and that further contribute to increasing soil complexity (Adl 2003).

A key functional role of soil biodiversity is its direct contribution to creating soil spatial structure. Moreover, as soil is a decisive factor shaping all terrestrial ecosystems we acknowledge, in accordance with Lavelle (2012), that soil variables, and especially the biogenic soil structure, are key factors regulating both aboveground and belowground biodiversity (Fig. 2.2). It follows that soil use and soil management are critical aspects of ecosystems management and largely determine the degree to which terrestrial ecosystems can support biodiversity, with cascading effects from local to global scales.

2.2 Soils as Complex Systems

Being complex systems, soils are obstructive to an analytic approach, which usually seeks to reduce a system to its elementary components and to comprehend direct interactions among these elements. The analytical approach is adequate for the study of simple systems mediated by linear interactions and ruled by general laws, such as gravity. For instance, knowing the mass of a falling object, its height and the gravitational constant allows predicting its speed and impact point. The elementary properties of simple systems are additive and relations between their elements mostly linear. On the contrary, complex systems are defined by a large diversity of components linked together by strong *feedback* interactions which in turn modify the initial state of the (eco)system. They are notably characterized by a *hierarchical*

Fig. 2.2 Cross-scale linkages between macroscopic surface characteristics and microscopic soil characteristics through spatial organization and functional biodiversity, *left*: from aboveground biodiversity to physic-chemical processes at the microbial scale, illustrating the role of soil functional biodiversity, and *right*: from soil use to the organisation of organic and mineral soil constituents at the microbial scale, illustrating the spatial organisation across spatial scales



organization, each level of the system being embedded within another. This approach is therefore also well adapted to soils where spatial structures vary from the molecular to the landscape scale, each level being formed by the elements of the lower level. Micro-aggregates coalesce to form macro-aggregates, which in turn are integrated in larger clods; further, specific structures define different types of horizons, themselves characterizing different types of soil (Fig. 2.3).

Each successive level is distinguished by newly acquired *emergent properties* and not by simple addition of lower level properties, and is defined by specific *temporal*

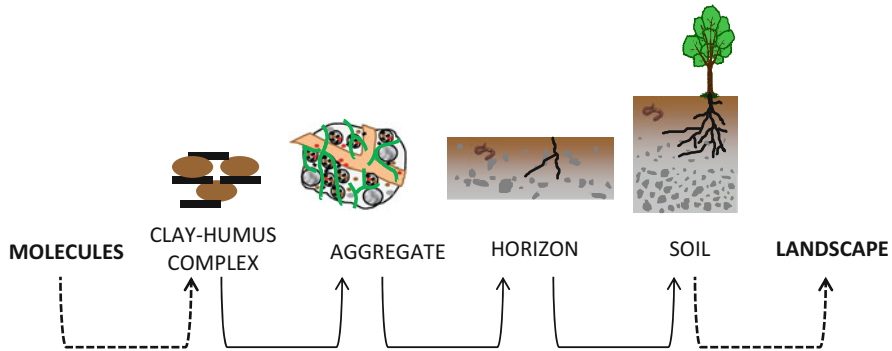


Fig. 2.3 Multi-scalar organization of soils (Modified from Gobat et al. 2004)

and spatial limits. Within soils, processes leading to development of aggregates are mediated by relatively small organisms (bacteria, fungi and micro-arthropods), acting at seasonal pace, but the effects appear also at larger time and landscape scales, for example when flood events are prevented by enhanced drainage due to increased soil porosity resulting from a greater abundance of soil aggregates. Other fundamental features of complex systems also characterize ecosystems' organization (Frontier et al. 2008) and can be successfully applied to the soil subsystem. The *homeostasis* concept, i.e. the property that tends to maintain a system or each defined level of the system in dynamic equilibrium conditions, has often been applied to ecosystems. Homeostasis results mainly from *negative feedback* effects, such as prey-predator relationships that regulate the soil communities.

Finally, soils are the main drivers in *self-organization* of ecosystems as they also shape the aboveground communities. Co-evolution of soils with the vegetation they support is mediated through changes in the quality and quantity of organic matter supplied by the vegetation, leading to acquired structure and self-organization which, theoretically, reaches its climax at the end of ecosystem succession. Young ecosystems, such as floodplains at the early stage of ecological succession, are characterized by a predominantly mineral abiotic environment with poorly developed biotic communities and weakly developed soil; their *resistance* (capacity to withstand disturbance) is therefore low. When the flood events become scarce/or the fluvial dynamic no longer exert a disturbing effect due to the construction of flood protection structures, alluvial ecosystems evolve towards the climax and acquire stronger aggregation due to earthworm activity, allowing increased resistance to further disturbance (*positive feedback*) (Bullinger-Weber et al. 2007). Inversely, mature ecosystems, such as temperate deciduous forests displaying well-established biotic communities and food-webs, particularly in the soil, show better resistance. However, when soil properties and functions are altered, as is the case of European forest affected by atmospheric nitrogen deposition resulting from the burning of fossil fuels and from agriculture, the capacity to resist perturbation is impaired. Enhanced N-deposition leads to both acidification and eutrophication that affect mycorrhization and fine root biomass. The storm "Lothar" in December 1999 caused unprecedented forest damage in Switzerland and the magnitude of the effect was partly attributed to reduced rooting due to the

altered soil status (Braun et al. 2003). Nevertheless, *resilience* (capacity to recover after major disturbance) may be preserved, due to the ability of soil communities to maintain basic functions of nutrient cycling even if the aboveground component of the ecosystem is subjected to major perturbation and temporarily destroyed (for example by fire, logging or storm) (Bret-Harte et al. 2013). Hence, there is a need to take into account all levels of the hierarchy, particularly soil organisms, as the emergent ecological properties and ecosystem functions and services at the scale of landscape ultimately link back to soil dwellers including microbes at the microphysical scale (e.g. Decaëns et al. 2006). The systemic approach, which considers a system in its totality and dynamic functioning, is therefore suitable for understanding ecosystems and thus, their most complex component: the soil (Ritz 2008).

Production and decomposition are the two main functions of soils related to plant growth (Brussaard et al. 2007). Both are defined by *biomass and energy fluxes* through the ecosystem, namely the food web. The aboveground part of a food web, involving mainly production and consumption, is often represented as pyramid-shaped with relatively simple interactions between primary producers, herbivores and carnivores of diverse levels. Such a vision is impossible to implement below-ground, as the relations between organisms responsible for decomposition are highly intertwined: here the notion of “web” is particularly appropriate to describe the complexity of interactions among the organisms responsible for organic matter transformations. This complexity mirrors the species diversity and the heterogeneity of the soil environment, as described in two aspects for bacteria diversity by Horner-Devine et al. (2004), and should be extended to whole soil habitat: on the one hand as structural heterogeneity, i.e. discontinuities in space and time and on the other hand as complexity in resources, conditions and/or interacting populations. The overwhelming complexity of (bio)physical, (bio)chemical and biological interactions in soils between environment and organisms or between organisms themselves prevents us from applying a solely analytic approach which concentrates on the elements and emphasizes the details.

Global perception, even if imperfect and partial, is an efficient approach and necessary condition when dealing with nonlinear and complex soil systems, including aboveground effects such as plant growth. However, due to the complexity of possible interactions among all biotic components and environmental factors one must acknowledge that exploring all these combinations is an impossible task (van der Putten 2009). Hence we must adopt a somewhat reductionist approach. As quoted by Andrén and Balandreau (1999), while looking inside the soil “black box” we have opened a “can of worms”; in order to reveal critical variables for plant growth we are now compelled to consider the system as a whole and accept its partly unfathomable features.

2.3 Soils as a Product of Species Diversity

Soils are alive. This somehow provocative statement underlines the fact that, unlike water or air, which are also considered as basic components of ecosystems, the very existence of soils is primarily defined by the presence of living organisms. They do

not just inhabit soils; they create them, almost entirely, at least for the upper part we mostly depend upon for growing food or fibre.

The prominence and functional significance of life in soils was acknowledged since the beginnings and the formalisation of soil science. Biota was indeed designed as one of the five factors of soil formation (Jenny 1941). Soils form as rocks break up and dissolve due to physical and chemical factors, but also with consistent contribution of soil organisms, including plants and fungi (Jongmans et al. 1997), releasing organic compounds, creating particles that bind with organic matter to form aggregates. Given the central roles played by soil dwellers in soil formation and functioning, soils can be considered as an emerging property of life. Soils are the product of a large array of biological processes and, contrary to air or water they depend for their structure and functioning on living organisms.

More than any other components of terrestrial and aquatic ecosystems, soils are subjected to the process of metabiosis as most soil organisms depend indirectly on others for their existence through modifications of their environment (Waid 1999). This form of ecological dependency has been well described in the case of earthworms (e.g. Tiunov 2007; Eisenhauer 2010), the ultimate ecosystem engineers. But a closer insight into soils reveals that a most soil organisms or soil functional groups are metabionts and modify the environment or supply resources, allowing dependent organisms to thrive. Examples include bacterial consortia and rhizosphere microbial feedbacks.

Despite substantial research efforts devoted in recent decades to the functional role of soil organisms in soil formation processes, progress remains limited by poor taxonomic expertise and methodological barriers, particularly for small-bodied taxa, such as bacteria or protists (Decaëns 2010; André et al. 2002; Pawlowski et al. 2012; Foissner 2008).

2.3.1 Functional Roles of Soil Dwellers

Underground organisms, including plant roots, participate in many ways in the formation and evolution of soils and also affect, directly or indirectly all above-ground ecosystem functions. For instance, agricultural productivity depends directly on soil borne organisms, which regulate nutrient availability and uptake, and indirectly on maintenance of soil structure and regulation of hydrological processes. Many other mechanisms underpin and support primary production and enhance nutrient release in the rhizosphere, particularly biochemical processes related to mutualistic interactions among microorganisms, mycorrhizae and plants, N-fixation through symbiotic bacteria, volatile-mediated plant growth promotion (e.g. Bailly and Weisskopf 2012), or abiotic stress tolerance through plant-growth-promoting rhizobacteria (e.g. Yang et al. 2009). On the other hand, plants themselves developed a sophisticated system of biochemical products allowing them to modulate in an antagonistic or synergistic manner various soil-borne pathogens (e.g. Pieterse et al. 2009). Clearly, all size categories of soil organisms contribute to some essential function (Table 2.1).

Table 2.1 Examples of diverse soil organisms within functional groups, related to their ecological functions and their main impact on soil properties and to their principal sphere of influence

Soil organisms	Functional group	Ecological function	Soil properties	Sphere of influence
Bacteria Archaea	Decomposers, nitrogen fixers, trace-gas producers	Nutrient cycling (e.g. N-fixation, nitrification, P-solubilisation, etc.) Decomposition Binding, weathering (release of organic compounds)	Mineral fertility Exchange capacity Structure, texture	Detritusphere, agregatosphere, rhizosphere, drilosphere
Fungi	Decomposers, symbionts	Iron oxidising/reducing Nutrient cycling Decomposition Release of binding compounds, enmeshing	Redox potential Mineral fertility Exchange capacity Structure	Detritusphere, agregatosphere, rhizosphere
Plant roots, lichens, bryophytes	Primary producers	SOM cycling, weathering	Texture, porosity, hydric regime, pH Structure	Rhizosphere, porosphere
Algae, diatoms, cyanobacteria	Primary producers	SOM cycling, weathering	Structure	Porosphere
Protista	Predators (bacteriophages) Decomposers	Biological population regulation Decomposition		Detritusphere, agregatosphere, rhizosphere, drilosphere
Nematoda	Plant feeders, predators (bacteriophages, fungivores, etc.)	Biological population regulation	Exchange capacity	Detritusphere, rhizosphere
Collembola	Saprophages, predators	Decomposition, biological population regulation	(Micro-)structure (faecal pellets)	Detritusphere
Acari	Saprophages, predators	Decomposition, biological population regulation	(Micro-)structure (faecal pellets)	Detritusphere
Enchytraeids	Saprophages, bacteriophages	Decomposition, biological population regulation, transportation	Structure (Micro-)porosity	Detritusphere, agregatosphere
Arthropoda	Predators, decomposers	Decomposition, biological population regulation, transportation	Structure (Micro-)porosity	Detritusphere
Earthworms	<i>Ecosystem engineers</i> ; burrowers, saprophages, geophages	Decomposition, formation of aggregates, transportation	Structure, porosity, hydric regime, clay-humus complex	Drilosphere

Compiled from: Lavelle (1996), Adl (2003), Gobat et al. (2004), Wall (2004), Brussaard et al. (2007), and Brussaard (2012)

The more recently developed ecosystem services concept (e.g. Wall 2004; Wall et al. 2010) also applied to soils aims to understand globally the interactions between soil biota and soil functions or functioning. This approach is mainly based on the distinction of taxa according to their effective body width. Even if this basically corresponds to a measure of the ability of different organisms to move through different soil pore size categories, it also reflects their impact on different soil processes. At the smaller spatial and temporal scales, the smallest sized organisms (microflora) are responsible for the digestion and transformation of complex organic molecules into simpler molecules and mineral elements available for plants uptake. Bacteria or fungi are responsible for most chemical processes controlling nutrient cycling (e.g. N-fixation, nitrification, P-solubilisation, iron-oxidation or reduction). Protozoa are also involved in many of these processes but this role is poorly studied and it is currently unclear how relevant they are in soil biogeochemical cycling (Finlay and Fenchel 1991; Ali et al. 2004; Hongoh et al. 2008; Risgaard-Petersen et al. 2006; Wilkinson and Mitchell 2010). On the other hand, the comminution (i.e. size reduction by fractionation) of fresh litter and the development of soil structural stability require longer time and are rather controlled by larger species, such as earthworms or arthropods which belong to the meso- or macrofauna. However, it is impossible to link the size of organisms to specific temporal and spatial scales; for example, the process of mineral weathering of parent material which occurs over a long period of time partly depends on organic acid production by many bacteria and fungi (Lavelle et al. 2006).

The degree of functional redundancy among soil organisms is an intensively studied and debated question and represents a challenge for the understanding of biodiversity-ecosystem function relationships. Some studies have shown there is no clear relationship between soil microbial diversity and microbe-driven functions (Griffiths et al. 2001; Nannipieri et al. 2003). A possible explanation is that diversity-function relationships exists only at the poor end of the diversity gradient while at higher diversities functional redundancy increases (Setälä and McLean 2004). Furthermore the degree to which diversity influences function may relate to resource levels (Philippot et al. 2013). For example, the degree to which microbial community structure controls C cycling in soil may differ between the rhizosphere or litter and the mineral soil because the rate limiting processes depend on resource availability (Schimel and Schaeffer 2012).

Effects of community composition may however be stronger than diversity changes *per se* if functionally important species are lost (Nielsen et al. 2011). The same could be true about overall biomass or abundance. Long-term data sets are highly valuable to address such questions but are unfortunately quite rare. Good examples include the DOK experiment in Switzerland (Maeder et al. 2002; Birkhofer et al. 2008) and the Rothamsted long-term research site in the UK (Glendinning et al. 1996). The vast majority of existing data are derived from experiments in controlled conditions over short time periods. A challenge with long-term observational or experimental studies is however to guarantee that results will be comparable over decades, especially for rapidly evolving methods such as molecular analysis of microbial diversity. Another challenge is that only a small fraction of biodiversity is usually studied in such programs (e.g. Maeder et al. 2002).

The current shortcoming of taxonomic knowledge about soil organisms and thus the lack of information on the precise functional roles of individual species prevents a detailed mechanistic understanding of functional consequences of biological interactions among soil organisms (Fitter 2005). One way to overcome these limitations is to use the functional diversity approach to study the multiple biological or biochemical interactions in soils. This can be achieved either by grouping species fulfilling similar functions in ecosystems, the so called functional groups (Brussaard et al. 2007), or by looking at specific communities of organisms acting at similar spatial and temporal scale, such as major regulator (e.g. earthworms or roots) (Lavelle 2000, 2002) (Table 2.1). While this approach clearly neither accounts for the full complexity of *soil functioning* nor for the diversity of soil organisms it nevertheless allows assessing the relationships between soil biota and functioning. This approach is especially useful to study ecological gradients and effects of natural or experimental perturbation of the soil environment.

2.3.2 *Plants Considered as Soil Dwellers*

Obviously, higher plants, at least their underground part, should also be included in the category of soil dwellers as they root in soils, influence physically and biochemically and play a major role in pedogenesis through their roots, their exudates and their aboveground and belowground litter quality and quantity. Thus, higher plants, as primary producers, are not just a part of the food chain; they also influence soil physico-chemical characteristics. They are active at all spatial scales but they interact most closely with other soil organisms in the direct vicinity of fine roots – the rhizosphere (Gobat et al. 2004). For instance, vascular plants are the main source of oxygen for the soil biota living in the proximity of small roots (Waid 1999) while old root channels allow preferential flow of water and air (Gobat et al. 2004; van Noordwijk et al. 2004). Rhizodeposition (lysates, exudates, mucilages, etc.) affect soil chemistry and especially nutrients concentrations in the vicinity of roots. Root biomass production can be higher than aboveground biomass, particularly in grasslands. For instance, the belowground biomass of a swamp meadow in Switzerland represented between 79 and 94 % of the total biomass (Buttler 1987). Chevallier et al. (2001) found that in pasture converted from sugarcane in Martinique root inputs were entirely responsible for an increase in organic carbon in the upper part of a vertisol. Some trees such as the cohune palm in Central America develop massive underground structures, roots and storage organs. Once dead, the decomposition of these organs creates large hotspots of organic matter and patches of moister soil as a result of the slow collapse of the surface (Kricher and Plotkin 1999).

Vascular plants are the main drivers of ecological linkages between aboveground and belowground subsystems (Wardle et al. 2004). At a global scale in non-disturbed environment, vegetation and soils have undergone a long ecological

co-evolution resulting in dynamically stable ecosystems (at the biogeocenosis level) characterised by complex interactions between abiotic factors (climate, parental mineral material, etc.) and biotic components. Plants have a lasting effect on the soil environment and evolutionary processes (e.g. how plants life history characteristics vary along succession stages) strongly influence pedogenesis and soil communities (van der Putten 2009). Thus, vegetation and soil as a biotic/abiotic subsystem are deemed to be in long-term equilibrium, mediated by feedback interactions; soils providing water and nutrient for plant growth; plants supporting the soil biota by organic matter inputs. However, the theory of hierarchical structure of ecosystems, with one particular level being embedded in another one of larger scale, leads to expectation that processes taking place at higher level will have significant effects on the lower one. Thus, as vegetation is also controlled by herbivores consumption, changes in plant community composition will affect the root-associated biota (Wardle et al. 2004). For example, Veen et al. (2010) reported that exclusion of cattle and rabbits from grassland changed the structure of nematodes communities more by altering vegetation composition than by altering soil abiotic characteristics. They hypothesised that these changes may result from effects related directly to living plant roots and indirectly to root exudates and inputs of organic matter. Plant-soil interactions are therefore a complex issue involving numerous and diverse feedbacks that occur between primary producers, consumers and decomposers (Bardgett 2005).

2.3.3 Soil Properties and Soil Organisms

Soils are usually described in terms of components, properties and processes, which are generally well known to soil scientists. These characteristics provide a decision-making framework for soil use. As soils are extremely heterogeneous, and cannot all fulfil the diverse societal needs, land management is sometimes – or at least should be – based on their suitability for specific uses (e.g. food and timber production, flood or landslide prevention). Land-use suitability planning refers primarily to basic soil properties (e.g. texture), to specific characteristics (e.g. depth) or to aggregated features (e.g. suitability for growing winter cereals). Soil biodiversity is approached through biological survey networks (e.g. Rutgers et al. 2009; Ranjard et al. 2010), but is generally not considered in land-use planning. Indeed, the functional link between soil properties and soil biodiversity is still not considered by policymakers and land-use planners and is only partly understood by scientists, although soil organisms, as pedogenic factor, are responsible for the major part of soil characteristics (Table 2.1).

There is no consensus on a standard list of physical and chemical soil properties (Baize 1993). Here we discuss those mostly related to plant growth, such as texture, structure, porosity, hydric regime, mineral fertility, etc. (Fig. 2.4). Soil temperature is not explicitly mentioned because it underlies most or all other properties and

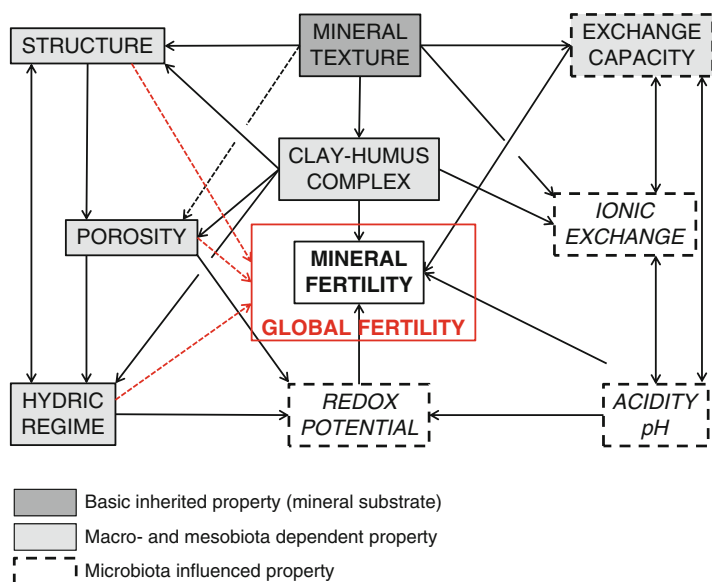


Fig. 2.4 The major soil properties depend mainly on biological activity and are therefore tied back to soil biodiversity. Some properties are prone to change in short-term (*in italics*) while others are more stable. Rapidly changing properties are mainly mediated by microbiota (Modified from Gobat et al. 2004)

influences them indirectly (Gobat et al. 2004). Some properties are purely physical (e.g. texture) while others reflect rather physicochemical and functional aspects (e.g. cation exchange capacity).

Soil textural composition refers to the respective proportion of mineral particles of different size (e.g. clay, silt and sand). It is inherited from mineral parent material and is the only soil property that is originally not influenced by living beings and by any other property. Soil texture is considered as a stable characteristic, although it is subject to long-term changes resulting from soil processes including biological weathering. All further considered soil characteristics depend directly or indirectly on texture (Ellis and Mellor 1995; Gobat et al. 2004), are connected by a system of complex interrelations and are more or less strongly dependent on biological activity (Fig. 2.4). Soil organisms are directly responsible for some properties including the granular structure of topsoil, which in turn determines porosity and hydric regime, and, the formation of clay-humus complex. Other properties are a product of the physicochemical inherited nature of soil modified by biological activity (e.g. pH or redox potential). The mineral fertility, on which plant growth relies heavily, could thus be considered as an emerging property of the soil system but even then, plant ion uptake depends on complex feedback mechanisms between rhizodeposition and the presence of microorganisms (ionic exchange). However, soil fertility is determined not only by mineral fertility but also on other soil properties (Fig. 2.4).

2.4 Aggregates as Functional Units

2.4.1 *Structure, a Key Property of Soils*

Structure is an obvious feature of soils. However, it is also probably the most difficult to measure objectively. Soil structure refers to the rearrangement of solid particles, both mineral and organic, into secondary particles called aggregates. These are primarily described in terms of size as macroaggregates ($>250\ \mu\text{m}$) and microaggregates ($<250\ \mu\text{m}$) and of shape. Depending on authors, macroscopic aggregates can be subdivided into five or more categories, usually including rounded granular structure, angular structure (prismatic, platy, blocky) and structure characterized by absence of aggregates (massive, single-grain) often inherited from parental material (Brady and Weil 2008; Ellis and Mellor 1995; Gerrard 2000; Gobat et al. 2004). Moreover, the degree of aggregation expresses the structure stability where the forces of cohesion between and within aggregates should be weak, moderate or strong. The size and the shape of aggregates are qualitatively appreciated by direct observation or with microscopy of thin sections (Dexter 1988; Oades 1993) while their stability can be quantified by measurement techniques (Le Bissonais 1996; Six et al. 2000; North 2006). Structure is a pivotal property in soil functioning. Structure degradation was identified in the European Strategy for Soil Protection as one of the eight major risks (Thot et al. 2008). Porosity, which refers to the size and patterns of structural voids (volume and connectivity between pores), influences the infiltration of water and air, the transfer of fluids such as leaching or water drainage which lead to soil differentiation. It also affects plant growth and roots penetration and more globally determines the suitability of life conditions for soil organisms. Unlike texture, structure changes over time; it is modified by changes in water and organic matter content, the degradation of stabilizing agents (e.g. breakup of macroaggregates, decay of hyphae or decomposition of bacterial poly-saccharides). Its persistence over time therefore depends on the balance between processes of formation and degradation.

2.4.1.1 Good Structure Versus Bad Structure

How can we define a good soil structure, and inversely a poor one? Implicitly, the beneficial aspects of soil structure are considered in relation to agricultural management practices and generally a “good” soil structure is associated with the organic matter content while “poor” soil structure is defined as absence or poor aggregation, for example in sodic environments (Nelson and Oades 1998). According to Dexter (1988) “good” structure is described by its stability and by the presence of all hierarchical orders of aggregates. However, in environments where the activity of earthworms is impeded by natural factors (e.g. arid climate), the soil organic matter content is naturally low. Likewise, soils characterized by the presence of dispersive cations (e.g. natural salinity or sodicity) and low aggregation rates cannot

be considered as “poor”. There is indeed a natural balance between soil properties, including structure and the soil biota and plants. “Loss” or “degradation” of the structure ultimately leads to the destruction of aggregates, leading to a single-grain structure (Brady and Weil 2008). On the other hand, as soil structure influences directly or indirectly all other soil properties, its loss or degradation is of crucial concern for human activities. Decreasing soil organic matter levels, compaction, salinization or reduction of soil faunal activity leading to structural degradation will ultimately result in economic losses and related social consequences (Nawaz 2013). The term “degradation” usually refers to detrimental changes in soil structure due to human activities and resulting in impaired aeration, water movement or root growth (Oades 1993).

2.4.2 Formation of Aggregates

The mechanisms involved in aggregates formation differ between the upper and the lower part of the soil. The rounded structure, more frequent in the topsoil is mostly a product of biological activity, while the characteristic angular structure of lower soil horizons stems from physical processes. Macroaggregates are one of the keys to plant establishment and growth (Wagner et al. 2007) since well-developed porosity associated with macroaggregates facilitates rooting and air supply as well as the biological activity of organisms responsible for organic matter degradation and thus nutrient supply. Macroaggregates also represent hotspots of microbiological activity and associated biochemical transformations (e.g. mineralization), as well as biological regulation by micro- and mesofauna.

2.4.2.1 Physical Mechanisms in Subsoil

Macroaggregates in the mineral, deeper soil horizons (B horizons) are typically angular. If the organic matter content is low, as is usually the case in the lower part of soils, wetting-and-drying cycles promote or enhance aggregation and give rise to a stable structure. This is mostly due to physical process of clay shrinking and swelling driven by hydrological changes. The main factors controlling this process are therefore clay content and quality (Baize and Jabiol 1995; Baize and Girard 2009; Girard et al. 1998; Ellis and Mellor 1995; Gerrard 2000; Wagner et al. 2007). The shrink-swell capacity is highest in smectite-rich clays (Oades 1993), and lower in kaolinite-clays (Murray 1999). Thus, the cohesive behaviour of clays is the dominant factor leading to the development of aggregates and cracks. The stability of such aggregates depends primary upon the strength and the persistence of drying/rewetting cycles (Oades 1993). Nevertheless, biological processes also influence this predominantly physical mechanism by enhancing the drying processes through root colonization of the soil and plant evapotranspiration.

Even if the origin of angular macroaggregates remains incompletely understood (Gerrard 2000), we can assume that the lower soil horizons mostly lack biologically-formed structure (Baize and Girard 2009; Girard et al. 1998). Physical forces involved in aggregates formation also include freeze/thaw cycles that lead mainly to platy structure (Brady and Weil 2008; Ellis and Mellor 1995). This structure can, however also be associated to direct or indirect biological causes (animal trampling, agricultural machinery). However, the effects of freeze-thaw cycles on structure or structural stability are ambiguous or nonlinear as they depend on numerous variables such as clay or organic matter content, moisture level, number of freeze-thaw cycles, and their complex interactions (see review in Six et al. 2004). Henry (2007) argues that many studies suffer from methodological weaknesses (e.g. using unrealistic temperature fluctuations) and thus that further investigations are necessary.

2.4.2.2 Biological Mechanisms in Topsoil

Biota mediated processes shape mostly, but not only, the structure in the upper part of soils. Numerous species, ranging from bacteria to macrofauna (namely soil engineers such earthworms, ants and termites) and plant roots, create various structures, which differ in size, stability and quality. Several factors (texture, clay mineralogy, cation content, crystalline and amorphous oxides and hydroxides) influence the effectiveness of aggregation but soil organic matter plays a crucial role particularly in structure stability (Bronick and Lal 2005; Abiven et al. 2009). Organic compounds increase the stability of aggregates by up to one order of magnitude but this depends on the quality of the organic constituents (Abiven et al. 2009). Labile compounds (e.g. released by bacteria) exhibit strong but transient effect on aggregate stability while more recalcitrant compounds (e.g. decomposed manure) have smaller initial, but longer-lasting effect. As aggregate stability is a critical factor of soil fertility, and soil organic carbon content is a manageable property, an adequate input of organic matter is the easiest way to maintain, enhance or restore the fertility of agricultural soils.

Several mechanisms lead to the formation of microaggregates, constituted primarily from organic molecules bound to clay particles by polyvalent cations. The release of extracellular polymeric compounds by bacteria binds these primary organo-mineral particles to form bacterial microaggregates. Similar processes were described involving fungus-derived polysaccharides (Chenu 1989) and glomalin, a glycoprotein released from arbuscular mycorrhizal fungi, which is thought to act as a “glue” due to its hydrophobic properties and thus to reduce aggregate breakdown during wetting and drying cycles (Miller and Jastrow 2000; Rillig and Mummey 2006).

The hierarchical arrangement of soil aggregates is the most common model to describe the process of aggregation with microaggregates being bound by organic polymers, that stick particles together, or are enmeshed by hyphae or plant roots to form macroaggregates (Dexter 1988; Tisdall and Oades 1982; Tisdall 1996; Miller and Jastrow 2000). In some soil types, however (Oxisol) stabilizing agents are

oxides rather than organic compounds (Oades and Waters 1991). Oades (1984) further hypothesised that microaggregates should also form within macroaggregate: as the particulate organic matter around which macroaggregates concentrically coalesce is decomposed, microbial exudates are released and microaggregates form inside (Bronick and Lal 2005).

At a larger scale, earthworms modify the soil structure by producing casts and forming large biopores. Other representatives of the soil macrofauna (termites, ants, spiders, larvae of insects, etc.) also contribute to the creation of soil porosity. Earthworms ingest mineral and decaying organic material and excrete stable macroaggregates, deposited on the burrow walls or on the soil surface (Brown et al. 2000). The stabilization of macroaggregates within casts, but also the formation and disruption of microaggregates within the intestine of earthworms, result from numerous physical, chemical and biochemical processes, involving also bacteria living in the digestive tract of earthworms (reviewed in Shipitalo and Le Bayon 2004). Where earthworms are scarce or absent (e.g. owing to unfavourable climatic conditions, acidity, etc.), the faecal pellets produced by microarthropods or enchytraeids influence the structure of upper organic horizons and can even make up the major part of forest litter layers, typically in moders (Rusek 1985; Lee and Foster 1991; Ponge 2003). Due to their small size (and weakness), microarthropods are usually unable to reach the deeper mineral or organo-mineral horizons and they are rather confined to pre-existing porosity (Lee and Foster 1991). The layers of accumulated faeces of epigeic fauna condition the development of specific communities and they become densely colonized by fungi (Oades 1993). The fungal community is dominated by ectomycorrhizal basidiomycetes, which allow the vegetation to take up nutrients sequestered in decaying litter and faecal pellets and released by detrital fungi and animals (Ponge 1990). Moreover, Lee and Foster (1991) observed in thin sections of faecal pellets a dense accumulation of bacterial cells. Lavelle (1996) suggests that these holorganic structures are incubators for microbial activities; when enchytraeids and arthropods re-ingest their droppings they also assimilate metabolites that have been released by the bacteria.

The above-mentioned interactions among soil organisms illustrate the complexity of interactions involved in the formation, stabilisation and disintegration of aggregates, which take place at different spatial and temporal scales (Six et al. 2004). The heterogeneity of the belowground habitat and functioning created by these multiple mechanisms can be compared to the complexity of the aboveground component of terrestrial ecosystems. This also shows that soil biodiversity is both a cause and a consequence of soil complexity. The belowground habitat should thus indeed be approached using a holistic view and a systemic approach.

2.5 Biodiversity as a Product of Soils

After the Rio Conference in 1992 and the popularization of the biodiversity concept, research on soil biodiversity gained momentum, especially with respect to its contribution to provisioning key ecosystem services (see Wall 2004). However, an

accurate estimation of specific soil biodiversity remains challenging because its assessment should include both organisms that spend their whole life in the soil as well as species that live only temporarily in the soil.

Gobat et al. (2004) propose a classification of soil animals based on the permanence or not in soils and their state of activity. Thus, temporal inactive geophiles, such as the caterpillars of many butterfly species, only bury in the ground for nymphosis; even so they constitute an important food source for other edaphic species. Temporal active geophiles, such as dipterans with edaphic larvae (e.g. Tipulidae), spend the first (and often longest) stage of life in soils, from egg to mature larva. Other species (e.g. scarabids) belong to periodic geophiles; although they spend their entire life in soil, if the ecological conditions become adverse they are able to change location through aerial dispersion. Finally, strict geobionts live permanently in soils and thus have low dispersal ability. Moreover, numerous species living in “soil annexes” i.e. aboveground structures such as dead wood, carrions or epiphytic soils, should also be considered as part of soil biota as they partake in organic matter “degradative successions” which eventually lead to soil organic matter cycling (Gobat et al. 2004). According to Decaëns et al. (2006), at least one quarter of all living species belongs to strict soil or litter dwellers, but bacteria and fungi are not covered by these estimations.

2.5.1 Heterogeneity of Habitats and Functions

The broad diversity of soil biota is closely related to the diversity as well as the spatial and temporal variability of soil types. Obtaining a reliable overview of soil heterogeneous habitats is therefore the first step and also a major challenge for global biodiversity assessment and assessment of its ecosystem functions.

Soils are spatially and temporally highly heterogeneous three-dimensional bodies, from landscape to micro-meter scale, and lower. They offer an overwhelming diversity of habitats for organisms, whose size varies from micrometre to decimetre. Soils could be compared to an underground jungle with a huge diversity of ecological conditions and niches. Mutual influences among soil organisms can be found across all scales (Ettema and Wardle 2002). As soils are spatially as well as functionally heterogeneous it is not surprising that soil organisms are studied in relation to their body size as well as to their functional roles. These two approaches are detailed hereafter.

2.5.1.1 Approach According to Body Size

Body size is related to the concept of ecological niche as many characteristics (e.g. feeding, locomotion and life modes) depend on the size and to the spatial domain of organisms (Gobat et al. 2004; Wolters 2000). The extreme variety of spatial dimensions and related ecological conditions create numerous and contrasted belowground “sub-ecosystems” which are as distinct as are forests or ponds in aboveground ecosystems.

For the microorganisms (size less than 0.2 mm), the soil is considered to be a semi-aquatic environment. The microbiota thrives within the water film around mineral particles or the interstitial soil water, which remains in micropores below the permanent wilting point. Prokaryotes, protists, small nematodes, rotifers and tardigrades are typical inhabitants of these micropores. Until now, the major part of taxonomic and functional studies focussed on microflora, i.e. bacteria (and archaea) owing to their central role in nutrient cycling. The prokaryotes are by far the most numerous group of organisms in soils (Torsvik and Ovreas 2002). In terrestrial systems, sediments and soil, they largely exceed their aquatic counterpart both in terms of biomass and density (Torsvik et al. 2002). This difference is most likely due to the structural heterogeneity and the complexity of soil resources (Torsvik et al. 2002; Horner-Devine et al. 2004).

The diversity, biogeography and specific functional roles of soil protists remain comparatively poorly studied despite significant advances in the understanding of the soil microbial loop and rhizosphere interactions (Bonkowski 2004; Clarholm 1981, 2005). Evidence for cryptic diversity (Heger et al. 2011; Kosakyan et al. 2012), restricted geographical distributions (Heger et al. 2013), strong impact on bacterial communities which can be contrasted even for closely related protists (Gluecksmann 2010) and likely unknown or under-evaluated role in biogeochemical cycles (Wilkinson 2008; Wilkinson and Mitchell 2010) suggest that a strong potential exists for significant discoveries on protists.

To what size category do fungi belong? This apparently simple question is actually not straightforward. Fungi are usually included in the microflora category but the hyphae influence soil properties and processes at a very large scale. One square metre of soil may contain up to 10,000 km of total length of mycelial filaments (Gobat et al. 2004) and Ritz and Young (2004) cite several studies stating that hyphal length is of the order $10^2 - 10^4 \text{ m g}^{-1}$ in arable, pasture and forest topsoils. Mycelial network, particularly in mycorrhizal symbiotic associations, plays a pivotal role in plant nutrition by translocation of water and mineral substances by exploring large soil volume and thus increasing the surface area for absorption. The role of fungi is also well recognized in the salient ecosystem process of soil aggregation (e.g. Rillig and Mummey 2006) as mycelia increase physically and biochemically the cohesion of particles. Their ramified structure and their products such as glomalin contribute largely to aggregates formation. Moreover, due to their ability to also grow through nutrient-impovertished zones and even through air (Ritz and Young 2004), the foraging strategy of fungi enables them to link remote places and to bridge different layers of soil such as the litter horizons and the rhizosphere. Hence, fungi are a perfect illustration of a paradoxically “minute” organism whose effects extend well beyond their size at higher functional ecosystem scales.

When compared with bacteria and fungi on one hand and macrofauna on the other, the mesofauna (length ranging from 0.2 to 4 mm) seem to suffer from the “middle-position child” syndrome and even if their diversity and ecological importance are recognized, comprehensive knowledge of these neither big nor small soil dwellers remains comparatively scarce. The role of mesofauna which usually

colonize the air filled pore system of soils (Lavelle et al. 2006) is rather examined in relationship to microorganisms on which they feed (e.g. Wolters 2000; Cole et al. 2004) as the decomposition rates are predator controlled (Vreeken-Buijs and Brussaard 1996) or in relationship to microstructure as the nematodes, collembolans, acari or enchytraeids, the main representatives of mesofauna, are typical producers and consumers of faecal pellets (Wolters 2000; Deschaseaux and Ponge 2001; Lavelle et al. 2006). In some cases, in a broad range of climatically different ecosystems, a whole organic upper layer may be made up by faecal pellets conferring this material its micro-granular peculiar feature (e.g. Loranger et al. 2003; Sadaka and Ponge 2003; Bernier and Ponge 1994). By producing these biogenic structures, microarthropods promote the activity of microbes, which would otherwise have very limited ability to move towards adequate substrates to decompose, and thus indirectly affect the global nutrient cycling (Lavelle et al. 2005).

Among macrofaunal organisms (length ranging from 4 to about 80 mm), earthworms, ants and termites, are known to enhance habitat heterogeneity mainly at the macrostructure scale. They are commonly designated as ecosystem engineers for they change the physical, as well as the biochemical soil conditions and therefore regulate the availability of biotic and abiotic resources (habitat, food, etc.), also to the benefit of other species (Jones et al. 1994; Lawton 1994; Jones et al. 1997; Eisenhauer 2010). Earthworms, probably one of the most studied group of edaphic invertebrates play a dominant role in pedogenesis by burrowing, ingesting soil and dead organic matter, excreting modified biogenic structures. In particular, soil structure is chemically and structurally reorganized during gut transit (e.g. Shipitalo and Le Bayon 2004). They are thought as being the most effective bioturbators, followed by ants and, to a lesser extent, termites (Paton et al. 1995). However, it is still not clear whether some soils have an extended burrow system because they provide appropriate conditions for earthworm development or if the earthworm activity improves the soil conditions (Kretzschmar 2004). Furthermore, following the reflections of Jones et al. (1994, 1997), Jouquet et al. (2006) discuss the differences between ants and termites being “extended phenotype engineers” (creating biogenic structures that directly influence their own needs) while earthworms mostly belong to “accidental engineers” (creating biogenic structures as a by-product of their movements through the soil in order to be as close as possible to their optimal environment). Nevertheless, both categories of soil engineers contribute to structural and functional heterogeneity of soils and influence to a large extent the global functioning. Besides the feedback loop effect and the creation of suitable conditions for other species (micro-, meso- and macroorganisms), vegetation is also dependent on these modifications in soil physical and biochemical properties. For instance, ants influence the composition of plant communities and increase overall species richness as some species tolerate better than others the repeated disturbance or seed predation and thus prosper on ant mounds (Carlson and Whitford 1991; Sebastia and Puig 2008). More generally, it is widely admitted that earthworm activities promote plant performance by a large array of processes including among others enhancement of oxygen and nutrient availability or physical accessibility to the roots (e.g. Brown et al. 2000). Other representatives of macrofauna include arthropods

with permanent or temporal edaphic stage, or gastropods and larger species of enchytraeids, which get involved in the first stages of the decomposition food chain, particularly in fragmentation (Gobat et al. 2004).

2.5.1.2 Approach According to the Function of Organisms

While the body size of some organisms is easy to define (e.g. a bacterium), this is not the case for many soil organisms. For example higher plants act simultaneously at different spatial and temporal scales (e.g. small rootlets, litter deposition or macroscopic aerial parties such as decaying trunks). The functional approach represents an alternative to the classification of organisms according to body size. This approach refers to the volume under the influence of soil organisms, which is determined by their ability to move through or occupy space (e.g. mobility of microbial or invertebrate species, extent of mycorrhizal hyphae or soil volume influenced by bacterial activity). This approach is useful to overcome the complexity of interactions between the aboveground and belowground parts of the ecosystems. It allows a better understanding of the global soil system and of ecosystem functions and services. The functional approach indeed represents a useful framework for the understanding and management of ecosystems.

Functional domains are characterized as “biologically relevant spheres of influence” (Beare et al. 1995). Although they occupy only ca. 10 % of the soil volume, they concentrate up to 90 % of the biological activities. This approach divides the soil functional complexity “black box” into smaller entities. The categories of functional domains broadly refer to soil biota communities sharing the same spatial and temporal environment and sharing similar adaptations.

The functional approach is analogous to the synusial approach based on the spatio-temporal organization levels to study vegetation (Gillet et al. 1990). A synusia is defined as a plant species assemblage characterized by uniformity of life form or height, having similar ecological requirements and occurring in similar habitat. Species belonging to one particular synusia thus occupy a similar spatial and temporal space. Several major functional domains or biological systems of regulation have been described (Beare et al. 1995; Brown et al. 2000; Lavelle and Spain 2001). Their characteristics (extension, origin, and role) vary over time and space. They are referred to as “hotspots of activity”. This approach is useful to study the complexity of the soil subsystem by considering smaller subsystems (Table 2.2).

Two of these functional domains (*detritusphere* and *rhizosphere*) are closely related to the plants, especially as organic matter sources. Plant debris is quantitatively the main aboveground input of organic matter although animal dejections and remains also represent a locally significant source. As plant productivity strongly depend on climate, the quantity of litter (*sensu stricto*) broadly varies among latitudinal gradients. Agricultural use of soils is the main factor modifying litter inputs qualitatively and quantitatively, with cascading impact on decomposer communities. For example, the replacement of temperate deciduous forest by cultivated land diminish annual litter fall from ca. 11 t ha⁻¹ to 0.3–2.0 t ha⁻¹ (Gobat et al. 2004, various sources).

Table 2.2 Functional domains in soil: main sphere of influence according to their origin and major soil functions and processes

Functional domain	Characterization	Role
Porosphere	Soil voids (macropores, mesopores, micropores)	Structural condition of soil, habitat for most of the larger invertebrate species, root penetration, air and water circulation
Aggregatosphere	Aggregated particles of different sizes and their immediate vicinity	Structural condition of soil, related to porosity; habitat for microorganisms and mesofauna
Drilosphere	Soil volume under earthworm influence (internal features in contact with the ingested soil and external structure created by earthworm activities)	Depends on the species and ecological categories of earthworms
Termitosphere	Termite nest and mounds	Changes in soil structure and chemical characteristics
Myrmecosphere	Ant nest and mounds	Changes in soil structure and chemical characteristics
Rhizosphere	Zone under the influence of the roots, immediate vicinity of rootlets	Biologically active interface; external boundaries indistinct, linked to the mycorrhizosphere and the hyphosphere
Detritusphere	Plant litter accumulation (upper organic horizons)	Corresponds to litter system (Lavelle and Spain 2006), habitat for epigeal communities

Compiled and adapted from: Linderman (1988), Andrade et al. (1998), Beare et al. (1995), Brown et al. (2000), Gobat et al. (2004), and Lavelle and Spain (2001)

Lal (2004) estimates, that conversion to agricultural ecosystems during both preindustrial and industrial eras led to depletion of the soil organic carbon by about 60 % in temperate regions and 75 % or more in the tropics. The losses of the original carbon pool are mostly due to i) the imbalance between outputs (yield) and inputs (manure), ii) accelerated mineralization provoked by tillage practices or iii) to the dominant form of soil degradation, i.e. erosion derived from the loss of soil structural stability (e.g. Morgan 2005; Pimentel 2006). The rhizosphere is often underestimated as a source of soil carbon and quantitative data are still scarce. The contribution of roots and mycorrhizae has been estimated to account for 63–70 % of total net primary production in coniferous forests where 4–5 times more material is returned to the soil by roots than by leaf and branch litter (Fogel 1983). The role of root decomposition in soil carbon sequestration and nutrient cycling is increasingly recognised (Silver and Miya 2001). But we still do not know much about the rates of root decay and how microbial communities and other soil organisms influence it. The rhizosphere is clearly the main interface between plant and soil. In this narrow zone directly influenced by root secretion (rhizodeposition) bacterial and fungal activities are especially high. The rhizosphere partly overlaps with the latter expanded concepts of *mycorrhizosphere* (distinguished from the rhizosphere soil around nonmycorrhizal roots) and

hyphosphere (affected only by the mycelium of mycorrhizal fungi), which induce presumably quantitative if not qualitative changes in microbial associated communities (Linderman 1988; Andrade et al. 1998).

Beside the rhizosphere, three other functional domains (*drilosphere*, *termitosphere*, *myrmecosphere*) are directly controlled by ecosystem engineers, which have evolved specific strategies to overcome the poor soil quality feeding resource and to evade abiotic adverse conditions such as density that can make foraging activities difficult (Lavelle and Spain 2001). These extended phenotype engineers (Jones et al. 1994, 1997) create patches of biogenic structures, more (nests of ants and termites) or less (earthworms' galleries) permanent and thus optimise their own living conditions while creating beneficial effects for other organisms (e.g. Jouquet et al. 2007).

The different functional domains, as described above and including the *aggregatosphere* and *porosphere*, are spatially and functionally superposed. For example earthworm activity contributes to creating porosity, which can be subsequently colonized by plant roots. Such synergistic or particular effects induce enhanced biological activity and they globally contribute to the awe-inspiring soil biodiversity.

2.5.2 Why Is Soil Biodiversity So High?

The quantification of biodiversity, notably at species level among soil organisms is far from being completed and both theoretical and practical aspects have still to be addressed. For example, species concepts, particularly those applied to micro-organisms are an issue not yet resolved, although recently developed molecular methods have a vast potential to overcome technical difficulties in sampling and quantifying the microbial functional diversity (Pankhurst et al. 1996; Pawlowski et al. 2012). Moreover, the functional role of soil biota has received considerable attention, as ecological processes seem driven more by the degree of functional dissimilarities among species than by the species number (Heemsberger et al. 2004). We suggest that understanding the reasons of the generally accepted overwhelming soil biodiversity and not only its state or its consequences, will be an important step towards sustainable soil and ecosystem management.

2.5.2.1 Spatial Heterogeneity

The theory of ecology postulates that species richness depends on the availability of niches; following the principle of competitive exclusion, the coexistence of species is only possible if their niches do not overlap. They must differ in at least one essential ecological factor such as their period of activity, their spatial repartition or their food source (Gobat et al. 2004). Thus, niche differentiation and resource partitioning in a given part of an ecosystem support strongly the diversity of species and the stabilization of communities' dynamics (Levine and HilleRisLambers 2009). The diversity of niches in the aboveground part of ecosystems is mainly determined by exogenous

physical and endogenous biotic factors; soil characteristics as an abiotic factor also contribute to aboveground diversity. However, at a smaller spatial level, soil regarded as a subset of the ecosystem supplies itself numerous spatial niches. Beside the general factors determining species diversity including among others inter- and intraspecific competition and ecosystem development stage, the soil specific spatial heterogeneity related to gradients in physical and chemical factors (pore dimension, water content and relative humidity, pH, soil atmosphere, texture, etc.) in both horizontal and vertical dimensions provides a major explanation for high soil biodiversity (Giller 1996). As discussed above, soil structure is the key property of soils, influencing and influenced by soil organisms. Thus, maintenance of agricultural productivity ultimately means maintaining soil structure and its role in key ecosystem processes such as decomposition, nutrient cycling and global soil fertility, all of which are mediated by soil organisms.

2.5.2.2 Food Resources

Based on the fundamental principle that energy flows through ecosystems, while elements cycle within the system, an ecosystem should be considered in terms of matter and energy coupled in the biomass. The primary source of energy in ecosystems is supplied through photosynthetic process and plants and algae are by far the main organisms able to convert solar energy into a chemical form of energy utilisable by heterotrophs. Solar energy can be considered as an unlimited resource but plant productivity is regulated by the availability of nutrients and water, and constrained by climate. All heterotrophic organisms are dependent on matter and energy transfer through trophic levels, from herbivores to higher predators, and energy contained in food is the principal limiting factor. The amount of matter – and thus energy – decreases from one level to the next by about a factor 10 as most of it is used for the metabolism or lost otherwise (dejections, necromass, etc.) (Lindeman 1942). However, the very end of the trophic chain is not achieved with the highest predators; the organic wastes (carcasses and dejections) enter the final stage of decomposition, humification and mineralization essentially performed by numerous and diversified soil biota. The reduction of energy at each successive trophic level, therefore the theoretical diminution of biomass along the food chain, is compensated in decomposition webs by increased quantity supply and partly trophic specialization. Although it has been reported that most of the soil organisms are trophically non-specialists, this view seems to be based on a limited number of studies (Giller 1996) and may also simply reflect our current ignorance of soil biota diversity (including cryptic species). All stages of food chain, i.e. primary production, herbivory, predation, parasitism and decomposition are also represented in soils, enabling unprecedented species diversification. Clearly, the trophic structure of edaphic communities does not correspond to a simple chain, but rather to an incredibly complex food web.

Gobat et al. (2010) propose a theoretical and simplified approach of the detritus web by describing three functional compartments corresponding to the size of organisms (Fig. 2.5). The two first compartments include macrofauna and mesofauna and are

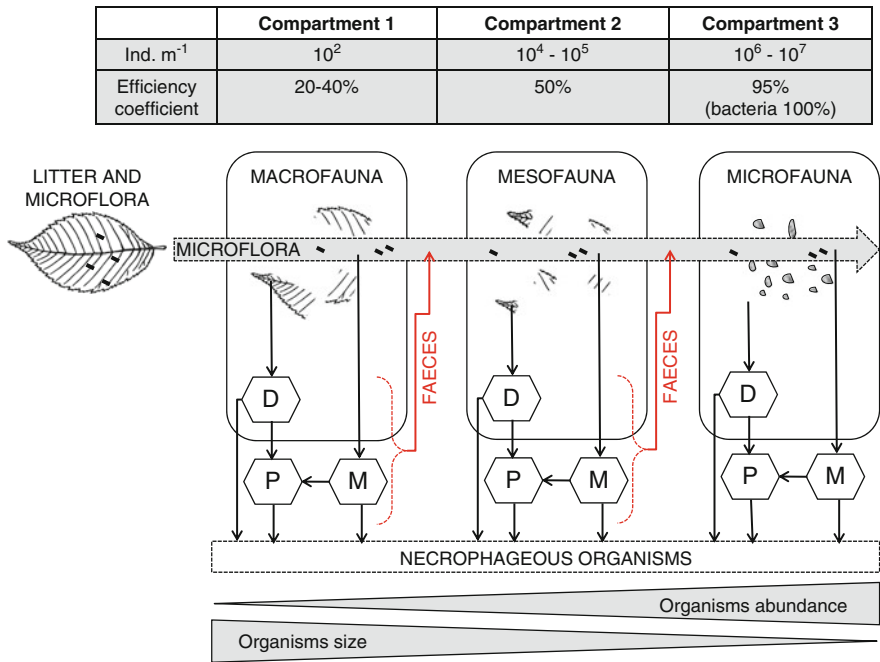


Fig. 2.5 Schematic and simplified soil detritus web through 3 functional compartments. **D** decomposers, **P** predators, **M** microphages (Modified from Gobat et al. 2010)

essentially characterized by fragmentation and burrowing processes, also by dispersion and selection of microflora present in the digestive tubes of the invertebrates. Biochemical processes mediated by microflora occur in the third compartment, which comprises mainly protozoa and micro-metazoa (nematodes, rotifers, etc.), acting as biological regulators of bacterial and fungal populations. In each compartment, organic matter is transformed, rejected as faeces and several times re-ingested. Predators and parasites are present at each stage; microphageous and necrophageous organisms enhance also diversity in the whole decomposition food web. Several features should be noted: (i) the permanent presence of microflora through the three compartments, (ii) the size of invertebrates and of plant particles diminish regularly, (iii) inversely, the abundance of organisms increases. Contrary to the aboveground food chain where the loss of energy is about 90 % between each trophic level, Gobat et al. (2010) ascribe to each compartment an “efficiency coefficient” which explains the species richness of decomposition food web. This coefficient with a value between 20 and 40 % in the first compartment rises up to 50 and 95 % respectively in the two successive modules and also explains why so many species can live in soils.

Actually, each food chain or web must start with a producer and, even if photo-synthetically active algae can be abundant on the soil surface or in large cracks of soils (Metting 1981), the major part of organic input in soils is based on plant production (aerial and roots inputs) on which both the grazer and decomposer food

chains depend. Lavelle (2012) states that on average 90 % of aboveground and belowground primary production ends up in the decomposition system, which is also enriched by the addition of dead soil organisms themselves. Furthermore, different qualities of soil organic material (fresh litter, organic residues, humic compounds) allow multiple feeding strategies and contribute to the diversity of soil food niches.

Soil communities' diversity and crucial soil functions necessary to humans depend therefore primarily on organic matter management regardless of the use of soil as organic matter is the major driver of soil biodiversity, and thus of soil ecosystem services.

2.6 Conclusion: Beyond Soil Science

Within the meaning of the theory of complex systems, soils may be considered as the ultimate emergent property of the Earth. They are the unique environmental medium where solid and fluid mineral and organic components merge to form original structures displaying specific and unpredictable characteristics such as the cation exchange capacity. We demonstrate that most of these characteristics are dependent on the aggregates, which in turn are closely linked to biological activity; aggregates are mostly formed by soil organisms and, in turn, determine habitat suitability for these organisms. Ecosystems functioning can be described in terms of fluxes of matter and energy, both being coupled in the biomass and transferred through the trophic chains. While the aboveground part of terrestrial ecosystems supports the primary productivity function almost all recycling processes, necessary to achieve the turnover of the matter, are provided by soils.

It is commonly admitted that soils contain a large proportion of the terrestrial biodiversity, higher than that of aboveground habitats. Spatial heterogeneity, defined by the structural state of soils, can explain, in part, the variety and quantity of suitable ecological niches leading to numerous adaptive strategies in terms of dwelling, moving, respiring and feeding of soil organisms. High resource availability and energy use efficiency in the decomposition food webs further explain the abundance and diversity of the soil biota. Actually, the highly fractal pattern of soils due to aggregation enhances the potential of exchange surfaces, necessary for transfers of matter and energy and thus for sustaining life. Due to this complexity, holistic reasoning constitutes an effective approach in soil science.

However, if complex thinking is essential to improving knowledge on soil functioning, two concomitant steps are to be simultaneously undertaken. On one side, ahead of the global understanding of the whole soil system, its components should continue to be identified and their place and contribution to the functioning clarified. In this respect progress is uneven. New molecular methods now allow major progress to be done on the inventory of soil biodiversity on a genetic level but the morphological, ecological and physiological characterisation of this diversity lags behind. Classical physical and chemical analyses of soils have a longer history but

a current challenge is now to link the newly discovered diversity of soil organisms to soil functions, structure, and chemical properties. This may imply the need to develop new approaches for the study of classical soil characteristics, or to adapt existing ones. On the other side, even if the complexity of soil is (largely) appreciated and (partly) understood, implementing this knowledge into sustainable management e.g. conservative agricultural practices implies facing challenges that cannot solely be overcome by soil scientists.

Some of the problems bound to the unsustainable use of soil are of a psychosocial nature and stem from diverse representations of the environment. In his book “The fear of the nature”, Terrason (1991) highlights the irrational fear of occidental civilizations for “nature” and especially for gloomy and humid places such as fens and marshes. By analogy, we consider that soils are an integral part of the “dark side” of the environment. Thus, although science should be addressed objectively soils and especially soil organisms are thus unconsciously ignored while defining priority research domains. Poor perception of visible soil invertebrates and of invisible microbes makes them appear repulsive, diverts attention from their study and slows down knowledge acquisition. A similar bias exists against botany according to Hallé (1999) who stresses the role of the emotional link (“zoocentrism”) between humans and the organisms they study, mainly vertebrates, who feed, breed, move and behave in “similar” ways as human do. Such irrational perceptions in turn lead to biased perceptions of the diversity of living organisms, their functional roles and complexity of life cycles or physiology. Although such an analysis appears seemingly inappropriate in the context of soil science, it underlines the latent perception shortcoming between soil scientists and the general public. Likewise, while exploring the reasons why French farmers do not integrate environmental measures into their practices, Weiss et al. (2006) brought to light the fact that the representation of the farmers’ own professional activity and the low level of credibility they give to scientific advice even if they are presented with figures are explicative of their behaviours.

These quite varied considerations imply that the involvement of social scientists in an interdisciplinary research (e.g. Bouwen and Taillieu 2004; Young et al. 2005) but also policymakers and stakeholders is proving to be the next challenge if we want to effectively promote awareness, propose operative solutions (Havlicek 2012) and strengthen the implementation of scientific results for a truly sustainable management of soils.

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Chapter 3

Beneficial Interactions in the Rhizosphere

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Abstract Production of plant biomass is one of the main ecosystem services delivered by soil. The area closely surrounding the root surface, the rhizosphere, is where plants interact with soil organisms. The interaction of a plant with soil microorganisms may result in several benefits to the plant, including improved nutrient availability or uptake, protection against pests and pathogens, improved tolerance to abiotic stress and growth promotion via hormones. Those relationships between plant and microorganisms determine plants growth and competitiveness. Ultimately the microbial community may determine plant community composition and succession. In this chapter we give an overview of fungal and bacterial microbial rhizosphere species that benefit plants, namely plant growth promoting bacteria, mycorrhizal fungi and other beneficial fungi. The aim is to summarize the current knowledge on mechanisms underlying plant-microbe interaction and to discuss the role of species identity and diversity for both microorganisms and plants. For each group (plant growth promoting bacteria, mycorrhiza, other beneficial fungi) we highlight the latest developments and promising future directions. At the end of the chapter the microbial groups are viewed as part of the soil ecosystem and interactions between the groups are discussed.

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3.1 Plant Growth Promoting Rhizobacteria

The discovery of plant growth-promoting rhizobacteria (PGPR) dates back to the end of the nineteenth century with the discovery of bacteria inside roots that could fix nitrogen; in the following 100 years several extracellular PGPR were detected (Gray and Smith 2005). Here we limit ourselves to PGPR that are associated with the root. Many PGPR are found on the root surface but a large number can also occur within the root, as endophytes (Hallmann et al. 1997). Most famous PGPR-containing phyla are Actinobacteria (e.g. *Streptomyces*), Bacteroidetes (e.g. *Pedobacter*), Firmicutes (e.g. *Bacillus*), and Proteobacteria (e.g. *Pseudomonas* and *Rhizobium*). Research focused mostly on crop plants, for the immediate benefits of increased yield or pest control in forestry, horticulture or agriculture. In addition, there is interest in the use of PGPR in extreme environments such as those in revegetation projects of desertified areas (Medina and Azcón 2012), or in reclamation of heavy metal-contaminated soils (Belimov et al. 2005). While the effects on plant growth are mainly studied for crop plants, the study of plant-microbe signalling is dominated by the model system *Arabidopsis* (e.g. Ryu et al. 2005). When screening for new PGPR several aspects have to be considered. Successful PGPR must be able to colonize the roots, and thus one can select for traits associated with root colonization. In addition, they should be safe to use by the growers (Köhl et al. 2011). Most screenings are done *in vitro*, testing a range of activities of single strains. The activities of interest are production of growth hormones, enzymes for nutrient uptake, production of siderophores and pathogen suppressing compounds. For practical reasons screenings are mostly done for single isolates, thereby neglecting species interactions that might affect biocontrol (Garbeva et al. 2011). This “community” aspect will be discussed further in relation to species diversity. We start with highlighting the many different mechanisms identified to cause plant growth promotion. Although the mechanisms are discussed separately, many species employ multiple mechanisms (Bashan and De-Bashan 2010) and relief of biotic and abiotic stresses can often not be studied independently.

3.1.1 Mechanisms: Nutrients, Protection, Hormones

3.1.1.1 Nutrients

There are several mechanisms by which PGPR can promote plant nutrition (Vessey 2003). Both nutrient availability and uptake might be increased; the latter is usually due to a change in root morphology in response to phytohormones. Nutrient availability might be increased directly by nitrogen (N) fixation, by producing enzymes that release nutrients, by production of siderophores that facilitate iron uptake, or indirectly by stimulating other symbioses. Bacteria which stimulate other symbioses are known as helper bacteria and have been found for both mycorrhizal (Frey-Klett et al. 2007) and rhizobial associations (Egamberdieva et al. 2010). Increased access

of plants to nitrogen by PGPR is mostly known from close associations between legumes and *Rhizobium* and secondly from free-living N-fixers for non-legumes. Many PGPR from different phyla are diazotrophs (organisms capable of living without external nitrogen source), yet increased nitrogen rarely has been identified as the main mechanism of plant growth stimulation (Dobbelaere et al. 2003). This could be a bias in the way PGPR are isolated or a consequence of the high fertilizer application in modern agriculture (Vessey 2003). For phosphorus (P) the main mechanism by which PGPR promote P levels in plants is via increasing availability rather than stimulating uptake (Richardson et al. 2009). Acidification and excretion of organic anions promotes the mobilization of poorly soluble P, but the relative importance of PGPR-acquired P for increasing plant growth remains doubtful (Richardson et al. 2009). The benefits of improved nutrient cycling by PGPR are obvious in terms of increased yield, but quality is also an important aspect. PGPR can increase micronutrients in the plant and thus produce more nutritious crops to alleviate malnutrition (Rana et al. 2012). Finally, partial replacement of chemical fertilizer application by PGPR serves many goals, including compensating for fertilizer scarcity and increased fertilizer costs as well as reducing environmental concerns such as nutrient runoff and water contamination (Yang et al. 2009; Vassilev et al. 2012).

3.1.1.2 Tolerance to Other Abiotic Stress

PGPR have also been shown to increase plant tolerance to a range of other abiotic stresses such as heavy metals contamination, water stress (flooding and drought), salinity and cold. Increased metal tolerance of plants due to bacteria is of great interest for phytoremediation (Gerhardt et al. 2009). There are many mechanisms by which PGPR can affect metal dynamics: they might affect bioavailability, uptake and transport within the plant. Metal-tolerant PGPR have been selected to increase plant biomass for phytoremediation; larger plant biomasses were achieved but metal concentrations in the plants were lower, possibly due to binding of metals to the surface of the bacteria (Dary et al. 2010).

One mechanism for relieving flood stress and drought stress appears to be similar, involving 1-aminocyclopropane-1-carboxylate (ACC) deaminase which has also been related to biotic stress resistance (Grichko and Glick 2001; Saleem et al. 2007). The breakdown of ACC, a precursor of ethylene, disturbs the stress-related hormone production in the plants (Hayat et al. 2010). ACC deaminase can be produced by many different PGPR, including *Pseudomonas* spp. and *Bacillus* spp. Effects of PGPR on drought stress are also mediated via antioxidants and cytokinins, which are involved in stomatal opening (Yang et al. 2009). Salt stress is often confounded with arid environments and there are a couple of reviews on the role of PGPR in abiotic stress amelioration (Yang et al. 2009; Dodd and Perez-Alfocea 2012). The reduction in ethylene via ACC deaminase seems to be very important, but other volatiles might also be involved (Yang et al. 2009), by affecting a transporter which controls Na⁺ uptake in the root. Increased tolerance to low temperature

has been found in wheat for a range of *Pseudomonas* isolates (Mishra et al. 2011). Grapevine (*Vitis vinifera*) plants colonized by *Burkholderia* sp. showed faster increases in stress-related gene expression and metabolite levels at low temperatures, while no effects of bacteria on plant parameters were observed at normal temperature (Theocharis et al. 2012). More extreme temperature and water regimes are associated with global climate change; a recent review of beneficial organisms under climate change showed general positive effects of PGPR on plant yield under drought but more mixed effects of elevated CO₂ on PGPR abundances (Compant et al. 2010).

3.1.1.3 Plant Protection

The improved nutrient status of the plants will generally improve plant tolerance to pests and herbivores, but PGPR are also known for more specific effects on pests and pathogens. The mechanisms vary from plant-mediated (induced systemic resistance: ISR), direct effects (antibiotics and volatiles) to indirect effects (rhizosphere or endophyte composition). Effects of PGPR inoculation on rhizosphere community composition seem relatively rare (Castro-Sowinski et al. 2007); hormone-induced plant signalling also had little effect on the rhizosphere (Doornbos et al. 2011) and thus rhizosphere-mediated effects of PGPR on plant protection need more empirical evidence before it can be accepted as a mechanism. A variation on the theme of indirect plant protection is the operating of PGPR via the resident endophytic community (Ardanov et al. 2012), but additional research is necessary to move from correlation to causation. Other PGPR direct effects on pathogens have been demonstrated via competition for nutrients (Lugtenberg and Kamilova 2009), production of antibiotics, lytic enzymes (Van Loon 1997) or volatiles such as cyanogen (Kumar et al. 2012). There appears to be little knowledge on the direct effect of PGPR-produced volatiles on pathogens, while there are many reports for other bacteria producing antifungal volatiles (e.g. Effmert et al. 2012). Some of the compounds that affect pathogens directly, e.g. 2,4-diacetylphloroglucinol (2,4-DAPG) have also been shown to induce plant defence (Weller et al. 2012) and thus it will be difficult to pinpoint the mechanism by which PGPR work. There are numerous examples of PGPR inducing systemic resistance, and ISR is part of many PGPR reviews (Lugtenberg and Kamilova 2009; Van Loon 1997).

3.1.1.4 Plant Hormones

Plant growth can also be promoted via production of growth hormones and this may influence resistance to biotic and abiotic stress. PGPR can synthesize plant hormones like indole-3-acetic acid (IAA) or modulate hormone production by the plant. Ethylene production by the plant is decreased when PGPR create a sink for ACC, a precursor of ethylene (Hayat et al. 2010). PGPR are routinely screened for ACC

deaminase activity or IAA production, but there are many more growth-promoting compounds associated with PGPR, including jasmonic acid (JA), salicylic acid (SA), abscisic acid (ABA), gibberellins (Gutierrez-Manero et al. 2001), zeatin (Cassan et al. 2009), rhizonin (Kang et al. 2010). In addition to the known plant hormones, there are volatile organic compounds from bacterial origin which promoted *Arabidopsis* growth (Ryu et al. 2003). It was found that volatiles from *Bacillus* affected auxin transport and cell expansion in *Arabidopsis* (Zhang et al. 2007). PGPR can also degrade hormones (Leveau and Lindow 2005) and the first bacterial genes for IAA degradation were only described recently (Leveau and Gerards 2008). Note that production of plant hormones by bacteria is not necessarily beneficial; also pathogenic bacteria synthesise IAA as essential part of their pathogenesis (Faure et al. 2009).

3.1.2 Role of PGPR Species Identity, Diversity, and Function

When PGPR species are combined, any outcome of the interaction is possible: decrease of the PGPR effect due to antagonism and increase due to additive or synergistic contributions of multiple species. Already in a single species, *Chryseobacterium balustinum*, it was shown that plant growth promotion worked via two pathways that were additive (Solano et al. 2008). For two *Bacillus* strains which produced different auxins it was confirmed that those auxins had additive effects compared to single auxins (Lim and Kim 2009). However, it is more common that the mechanisms differ strongly between species. Valverde et al. (2006) found synergism between *Mesorhizobium* and *Pseudomonas* inoculation in the field, but in greenhouse studies the opposite was found: combined inoculation was less effective than single inoculations. This shows the importance of the context for outcome of species interactions. Combined species inoculation could also be applied to increase reliability rather than total yield, assuming that there is functional redundancy and that at least one of the inoculated isolates is suited to the local conditions. Here again one needs to be sure that there are no antagonistic effects between PGPR. For instance, Felici et al. (2008) studied effects of *Bacillus subtilis* and *Azospirillum brasilense* alone and in combination on tomato and found that the combination did worse than the single inoculations. The abundance of the bacteria was not different between single and dual inoculations and thus the explanation is sought in conflicting molecular signals (Felici et al. 2008).

Most PGPR studies focused on agricultural conditions where plant monocultures are predominant. Yet, with PGPR that may have differential effects on plant species, it is clear that they potentially can have strong effects on plant community composition and diversity. This might be exploited by selecting PGPR that promote crop growth while inhibiting weed germination (Martinez-Mendoza et al. 2012). However, we did not find any paper studying effects of PGPR on plant community richness; in natural situations PGPR are not studied as such.

3.1.3 Latest Developments

In the field of PGPR application there is a shift from mass inoculations with one or two beneficial species to stimulating local beneficial organisms (Chaparro et al. 2012). The latter are adapted to the *in situ* environmental conditions, whereas the former can be considered as invaders that will have a hard time getting established within the indigenous microbial community. The study of local beneficials has been enormously facilitated by methodological developments, such as next generation sequencing which enables species identification at higher resolution than before. Real-time PCR has been applied to investigate the natural occurrence of PGPR in wild *Hordeum* (Timmusk et al. 2009) while high throughput sequencing provides insight into the variety of species present in the rhizosphere, and especially the many species that occur at low densities. Many of those rare species might be potential PGPR, but it is unknown whether they function at such low abundances in this diverse context. The trend has been to focus on dominant and/or easily cultivable species when studying plant-microbe interactions. Recent empirical work demonstrated that loss of rare microbes also affected plant growth (Hol et al. 2010). Other developments are in the area of species interactions. Inter-specific interactions between bacteria determine their gene expression (Garbeva et al. 2011); knowledge of the changes in gene expression when bacterial species are growing together could help predict the success of combining PGPR. There has been much progress in the research on PGPR induced plant signalling, but it is unclear whether PGPR application rate and success has also benefitted from that knowledge. To some extent the knowledge is applied by genetically modifying PGPR: an ISR inducing protein from a pathogenic bacterium was introduced into a known PGPR *Bacillus subtilis* and this resulted in synergism of gene expression for plant cell growth and plant defense related genes (Wang et al. 2011).

3.2 Mycorrhizal Fungi

Mycorrhizal symbiosis is recognized as a key component in terrestrial ecosystems. About 80 % of the terrestrial plant species are commonly mycorrhizal (Smith and Read 2008). The taxonomic position of the host plant and the mycorrhizal fungi characterize the types of mycorrhizal symbiosis (Finlay 2008). In this chapter we will mainly focus on Arbuscular Mycorrhizal (AM) fungi and Ectomycorrhizal (EM) fungi representing the major mycorrhizal associations in natural ecosystems. EM fungi often form the dominant microbial components of forest ecosystems in the boreal, temperate and Mediterranean climate zones, characterized by low nutrient availability and tree productivity (Smith and Read 2008). They can be formed by both Basidiomycota and Ascomycota and it is estimated that 7–10,000 fungal species can form ectomycorrhizal associations with 8,000 plant species globally (Taylor and Alexander 2005). AM symbiosis has a widespread distribution, being

formed with a very wide range of plant species, as many as 250,000 in very different ecosystems (Brundrett 2009). Formation of AM fungi is highest in field layers of temperate deciduous forests, in tropical forests soils and in grasslands (Read and Perez-Moreno 2003). AM fungi form a distinct phylum, the Glomeromycota (Schüssler et al. 2001). Despite the abundance of Glomeralean fungi, only 150–250 species have so far being distinguished on the basis of spore morphology, but DNA-based studies indicate that the true diversity of these symbionts may be higher (Fitter 2005).

3.2.1 Mechanisms: Nutrients, Protection, Hormones

3.2.1.1 Nutrients

Arbuscular and ecto-mycorrhizal fungi assist the plant in the uptake of mineral nutrients by means of an extraradical mycelium (Smith and Read 2008). The extraradical mycelium can be more efficient in exploring the soil than the roots due to the small diameter of the hyphae which on the one hand allows access to microsites that are inaccessible for plant roots and on the other hand increase the surface area for nutrient uptake. This is especially important for nutrients like phosphorus with low mobility in soil. The enhanced plant P nutrition is the best known benefit of the arbuscular mycorrhizal symbiosis. It has been shown that acquisition of P via the AM fungi down regulates direct P uptake by the plant. Therefore, contribution of AM fungi to P acquisition is significant even in plants which do not show an increase in total P uptake and/or growth (Smith et al. 2004). Apart from P uptake, AM fungi can transfer other nutrients like N, Zn, Mg and Ca to the plant. N can be taken up by the AM fungi in the inorganic forms of NH_4^+ and NO_3^- and in the organic forms as amino acids and they can subsequently be translocated to the roots (Govindarajulu et al. 2005). Due to the high mobility in soil of NO_3^- the scavenging ability of AM fungi does not provide any advantage to the plant. In addition, also the suggested ecological significance of NH_4^+ and amino acid uptake by the fungus remains uncertain and needs further research (Hodge et al. 2010).

More and more attention is given to the role of mycorrhizal fungi to mobilize nutrients from organic and mineral substrates. Ericoid and EM fungi may play a significant role in heathlands and boreal forest ecosystems by mobilizing N and P from organic forms which are not readily available to plant roots (Read and Perez-Moreno 2003). EM fungi are able to produce a large range of extracellular and cell wall-bound hydrolytic and oxidative enzymes which degrade N- and P- compounds contained in soil organic matter (e.g. Buée et al. 2007, 2009). The role of AM fungi in their capacity to mobilize organic substrates is nevertheless unclear so far. Hodge et al. (2001) reported that AM fungi extraradical mycelium facilitated N capture from litter, although it has been suggested that this was an indirect effect via stimulation of decomposers. The ability of AM fungi to mobilize P from an organic form has

been shown under axenic conditions (Koide and Kabir 2000). There is still no evidence of phosphatases production by the fungus in soil, but the external AM mycelium may increase phosphatase exudation by roots or other microorganisms (Joner and Jakobsen 1995).

EM fungi contribute to nutrient availability as well by actively releasing nutrients from mineral particles and rock surfaces (weathering) (Van Hees et al. 2006). Wallander et al. (2002), using particle-induced X-ray emission (PIXE) analysis of elements contents of fungal rhizomorphs, showed that an ectomycorrhizal *Rhizopogon* species had the ability to mobilize significant amounts of P and K from the minerals apatite and biotite. The production of oxalate is one of the mechanisms by which several EM can dissolve minerals (Courty et al. 2010). There is no evidence of the weathering capability by AM fungi but Arocena et al. (2012) found that the presence of AM fungi increased the transformation of biotite by the plant.

3.2.1.2 Plant Protection Against Herbivores and Pathogens

Mycorrhizal fungi can protect plants against insect (Hartley and Gange 2009) and nematode (Hol and Cook 2005) pests and pathogens (Jung et al. 2012). Different mechanisms for plant protection by mycorrhizal fungi have been suggested involving the induction of changes both in the host plant and in the rhizosphere. AM fungi can modify root exudates such that zoospores of the plant pathogen *Phytophthora nicotianae* are attracted or repulsed, depending on root age (Lioussanne et al. 2008). Root exudates from mycorrhizal tomato plants temporarily paralyzed nematodes and decreased the penetration of nematodes into mycorrhizal roots (Vos et al. 2011). Changes in soil microbial community mediated by AMF can also facilitate performance and survival of biocontrol bacteria in the rhizosphere (Harrier and Watson 2004). In this respect, Li et al. (2007) found that mycorrhiza-associated bacteria from the genus *Paenibacillus* showed biocontrol abilities against *Pythium* damping-off in cucumber plants. Besides the recognized improvement of plant resistance to biotic and abiotic stresses via an enhancement of plant nutrition by mycorrhizal fungi (Azcón-Aguilar and Barea 1996), there is growing evidence of induction of changes in plant morphology and composition as well as in plant defence pathways. Systemic protection is mediated by phytohormones like jasmonic and salicylic acid. The activation by mycorrhizal fungi of plant immune responses leads to a primed state of the plant that allows a more efficient activation of defence mechanisms. The systemic protection has been confirmed in the root system against nematodes (Hao et al. 2012) and bacterial and fungal pathogens (Khaosaad et al. 2007) as well as on pest and pathogens attacking the shoots. Although the outcome of the above-ground interactions can be quite variable, mycorrhization in general had positive effects on the attraction of beneficial insects like pollinators and parasitoids (Jung et al. 2012). However, we should bear in mind that the ability to enhance resistance/tolerance depends on mycorrhizal fungal isolates, pathogens and environmental conditions (Pozo and Azcón-Aguilar 2007).

3.2.1.3 Tolerance to Abiotic Stress

Drought and heavy metal contaminations are important abiotic constraints for plant development and survival. Several studies have shown that mycorrhizal fungi improve plant protection from those stresses, recently reviewed by Azcón et al. (2013). Mycorrhizal fungi isolated from heavy metal contaminated sites have been shown to cope better in contaminated soils than those strains isolated from non-contaminated sites (Fomina et al. 2005; Medina and Azcón 2010). These authors stress the importance of using tolerant isolates in reclamation/remediation programs. Some of the mechanisms by which mycorrhizal fungi confer tolerance to plants to abiotic stress involve the activation of antioxidative detoxification systems (superoxide dismutase, catalase, total peroxidase or glutathione reductase) (Bellion et al. 2006). Since metals cannot be degraded they must be transformed to less toxic forms or immobilized to prevent their incorporation in the food web. Immobilization has been demonstrated by the production of extracellular and intracellular chelating compounds (tricarboxylic acids, proteins) and cell-wall binding proteins (Fomina et al. 2005; Gonzalez-Guerrero et al. 2006). Mycorrhizal fungi have also been shown to increase plant resistance to water and salinity stress. It has been demonstrated that plant aquaporins are regulated by AM symbiosis, which results in a facilitation of water transport between the fungus and the root and contributes to plant tolerance to stress conditions (Ruiz-Lozano and Aroca 2010). Aquaporin expression induced by EM fungi seems to manifest particularly during droughts or other environmental stresses like low soil temperature. These are common situations in many of the habitat areas of EM fungi (Lehto and Zwiasek 2011). An important physical factor controlling water transfer to the plants is the soil structural stability. Arbuscular mycorrhizal fungi have been shown to have a positive impact on soil aggregates. Different mechanisms contribute to the formation of aggregates by the fungus, including physical binding by the hyphae and fungal proteins such as glomalin (Rillig and Mummey 2006).

3.2.2 Role of Mycorrhizal Species Identity and Diversity

One of the most challenging questions faced by ecologists is whether there is a general relationship between biological diversity and ecosystem function. As rates of both species extinction and invasion appear to be increasing, the importance of establishing whether biodiversity *per se* is important for ecosystem function has become a central issue in ecology. Mycorrhizal fungi functional diversity is, therefore, key to understanding their contribution to ecological ecosystem processes. The functional redundancy assumption for mycorrhizal fungi is more and more under debate. This is supported by the growing evidence that mycorrhizal fungi are more host-plant specific and functionally complementary than it was thought. In a field experiment, Vandenkoornhuyse et al. (2003) reported the presence of different AM communities in co-existing grass species and Croll et al. (2008) reported strong

host preferences by AM genotypes from a single agriculture field. Host specificity by EM fungi has been shown more often than by AM fungi (Nara 2006; Walker et al. 2005). These host specificity interactions are dependent on host phylogenetic distance, plant life-history traits and physiology and successional strategies of both host and fungi (Smith et al. 2009). A number of experiments using different assemblages of mycorrhizal communities involving composition and diversity of mycorrhizal fungi, have been carried out to compare their effects on plant diversity and productivity. Van der Heijden (2002) proposed that the way in which AM fungi influence plant communities, either by promoting plant competition or coexistence, depends on the number and relative abundance of mycorrhizal-dependent plant species in the species pool of a community. Host specificity and mycorrhizal functional diversity are aspects intimately related to this mechanism and have, therefore, the potential to influence plant community structure. For instance, one symbiont might be a better competitor for a certain trait, e.g. nutrient uptake or, plant protection, and might more efficiently deliver these benefits to a single host species. Another way via which mycorrhizal fungi may influence plant diversity is by means of the external mycelium. In any given plant community, it commonly appears that mycorrhizal fungi form extensive networks connecting multiple plant species. This external mycelium can have an impact on plant competition by facilitating seedlings establishment and survival near mycorrhizal plants (Booth and Hoeksema 2010). The common network also allows transfer of nutrients and water between plants (Egerton-Warburton et al. 2007; He et al. 2006) and it has been suggested as a mechanism for influencing plant competition by minimizing fitness differences between plant species. However, the ecological significance of the common mycelium network needs further research (Hart et al. 2003). Increasing diversity of mixed populations of mycorrhizal fungi provides more beneficial effects on plant productivity and/or diversity suggesting that they are complementary in their functions (e.g. Gustafson and Casper 2006; Jansa et al. 2008; Maherali and Klironomos 2007). Functional variability among mycorrhizal species has also been proposed as an indication of complementarity between the different mycorrhizal species. For instance, it has been shown that enzymatic capabilities, such as production of extracellular phosphatases or proteolytic enzymes, or the ability to produce organic acid as a mechanism of mineral weathering, can vary depending on the EM species and even on the strain (Buée et al. 2005; Nygren et al. 2007). Variation between mycorrhizal species or isolates also exists in the efficiency of bioprotection (Sikes et al. 2009), in strategies to acquire P from the soil (Smith et al. 2000), to tolerate biotic stress (Helgason et al. 2007), or to adapt to environmental conditions (Di Pietro et al. 2007; Lekberg et al. 2007).

3.2.3 Latest Developments

One future challenge is to identify the functions fulfilled by assemblages of mycorrhizal fungi in the field. This will help us to elucidate the role of mycorrhizal diversity in ecosystems and to consequently evaluate the impact of human activities

or global warming on ecosystem processes. A pre-requisite of such large-scale functional ecology studies is to distinguish between individuals within a mycorrhizal community. Development of new molecular tools has led to new molecular phylogenetic classifications that facilitate us to explore the biodiversity of mycorrhizal fungi in the field. However, it is not known yet to what extent those phylogenetic groups correspond with functional and ecologically relevant units (Sanders 2004). There is emerging evidence that assemblages of genotypes may affect ecosystem processes to a similar extent as assemblages of species. Since the species/genotype concept of mycorrhizal fungi is poorly understood it is difficult to link species and traits. Some genomes of mycorrhizal species are already sequenced and a number of other species and strains of mycorrhizal plants and fungi are in process to be sequenced (Johnson et al. 2012). This will help us to reveal differences between species and genotypes, to identify functional gene markers targeting key traits of mycorrhizal fungi which will facilitate us to elucidate the importance of mycorrhizal diversity on ecosystem functioning.

3.3 Other Plant Growth Promoting Fungi

Besides the mycorrhizal fungi there are more fungal groups occurring in the rhizosphere which have positive effects on plant growth, e.g. endophytes (Schardl et al. 2004; Porras-Alfaro and Bayman 2011), non-pathogenic *Fusarium* spp. (Lemanceau and Alabouvette 1991), and *Trichoderma* spp. (Hermosa et al. 2012). These other plant growth-promoting fungi have a wide taxonomic background and cover a wide range of plant benefits. For instance, grass endophytes are associated with improved drought resistance and herbivory resistance via secondary metabolite production while *Trichoderma* spp. are mostly known as hyperparasite of plant-pathogenic fungi. Some fungi have only recently been identified as plant growth promoters: soil-inhabiting entomopathogenic fungi (e.g. *Metarhizium*) can also be plant endophytes which antagonize plant pathogens and/or stimulate plant growth (Vega et al. 2009). The research focus is broad, depending on the fungal species: *Fusarium* and *Trichoderma* are often investigated in an agricultural/horticultural context, while dark septate endophytes feature more often in natural ecosystems (Newsham 2011).

3.3.1 Mechanisms: Nutrients, Protection, Hormones

3.3.1.1 Nutrients

Dark septate endophytic fungi (DSE) are a miscellaneous group of root-colonizing fungi which generally have positive effects on plant growth (Newsham 2011). The role of DSE in plant nutrition is often described as unclear (Zhang et al. 2012), but in general DSE increase plant biomass and nutrient content, especially when organic nitrogen is available (Newsham 2011). Thus some contribution to nutrient

supply to the plant could be expected. Instead of increasing nutrient availability, there are also indications that DSE increase nutrient use efficiency (Alberton et al. 2010). In tree species DSE show similarities with mycorrhiza (Peterson et al. 2008), but DSE appeared to occupy different niches as compared to AM and EF (Wagg et al. 2008). For other fungi complex nutritional relationships were found, depending on nitrogen and phosphorus concentrations. *Clonostachys rosea*, a biocontrol fungus that can grow both as free-living saprophyte and endophyte, increased P and decreased N in tomato (Ravnskov et al. 2006). Mechanisms have not been tested but the authors speculate about increased P solubilisation. Li et al. (2012) found an interaction between N and P availability for endophyte-grass symbiosis: the endophyte infection improved acid phosphatase activity of endophyte-plants but only when sufficient nitrogen was available. Saprophytic fungi can stimulate organic matter decomposition and thus increase nutrient availability for the plants (Buée et al. 2009).

3.3.1.2 Plant Protection Against Herbivores and Pathogens

ISR has been found for a wide range of fungi, including e.g. *Trichoderma*, *Fusarium*, *Penicillium*, *Phoma* and *Pythium* (Shoreish et al. 2010; Trillas and Segarra 2009). *Aspergillus ustus* induced systemic resistance against *Botrytis* and *Pseudomonas syringae*, probably via jasmonic acid, salicylic acid, ethylene and camalexin defense related genes (Salas-Marina et al. 2011). *Trichoderma* in tomato up regulates SA and this appears to be related to stronger JA response after *Botrytis cinerea* infection (Tucci et al. 2011). *Beauveria bassiana* can induce ISR against pathogenic bacteria and also the fungal entomopathogen *Lecanicillium* (Ownley et al. 2010) appears to be capable of inducing ISR. Non-pathogenic *Fusarium* is initially perceived by a plant as pathogenic but the association with ectosymbiotic bacteria is essential to maintain the non-pathogenic status (Moretti et al. 2012). Other mechanisms of plant protection include competition for space or nutrients or the production of antimicrobial substances. Some compounds are produced directly by the fungi themselves, e.g. antibiotics, while other fungi are inducing secondary metabolites in the plant. Finally, a rather indirect mechanism by which saprophytic fungi could offer plants protection is by selecting for antifungal rhizobacteria (De Boer et al. 2008). The presence of many saprophytic fungi would select for antibiotic producing bacteria which in turn protect the plants against plant-pathogenic fungi.

3.3.1.3 Tolerance to Abiotic Stress

Improved drought stress resistance by grasses infected with endophytes is one of the most famous examples of fungi relieving abiotic stress. Also salt resistance can be improved by *Neotyphodium* endophytes (Sabzalain and Mirlohi 2010). Tolerance to abiotic stress might share the same mechanism, as suggested by Torres et al. (2012) who suggested that oxidative stress protection is the fundamental mechanism of drought tolerance, heavy metal tolerance and others. Hamilton et al. (2012)

hypothesized that reactive oxygen species and antioxidants are crucial in symbioses between plants and fungi and suggested that they determine the outcome between pathogenicity and mutualism. A completely different mechanism of plant growth promotion is the ability of *Trichoderma* to degrade allelochemicals in the rhizosphere and thereby improving yield under continuous cropping systems (Chen et al. 2011).

3.3.1.4 Plant Hormones

The many aspects of plant hormones in relation to other organisms are reviewed by Pieterse et al. (2012). Fungi can synthesize hormones themselves or influence hormone production in plants. It is not always easy to judge how important the hormone production is for the net effect on plant growth. *Aspergillus ustus* does promote plant growth and can synthesize auxins and gibberellins. However, it was also able to promote plant growth in hormone defective mutants (auxin, ethylene, cytokinin or abscisic acid), and thus *Aspergillus* has other mechanisms that might be more important than hormone production (Salas-Marina et al. 2011). *Trichoderma* has ACC deaminase activity, similar to what was described for PGPR above, and silencing of that gene decreased root elongation promotion of the mutants on canola seedlings (Viterbo et al. 2010). Lahrman and Zuccaro (2012) describe the ability of the root endophytic fungus *Piriformospora indica* to manipulate the host plants hormones as part of early colonization, which later results in plant growth promotion.

3.3.2 Latest Developments

Compared to PGPR and mycorrhizal fungi the other beneficial fungi are a more diverse group and as such it is more difficult to summarize the latest developments in the field. New plant-growth- promoting fungi keep being isolated, and sometimes they are already known for some other benefits like the entomopathogenic fungi. The current knowledge about the mechanisms is not sufficient to determine which ones are unique in comparison to PGPR and mycorrhizal fungi. New applications of biocontrol agents could be made by introducing genes from fungi into plants. *Trichoderma* genes for heat shock proteins introduced in *Arabidopsis* increases heat resistance (Montero-Barrientos et al. 2010).

3.4 Interactions Between Mycorrhizal Fungi, Other Fungi and Rhizobacteria

The separate discussion of those beneficial organisms in different sections provides structure but there are overlaps and connections between the groups of organisms. Positive interactions between rhizosphere microorganisms seem to be dependent on

the functional compatibility between them. Different AM fungal strains have been shown to have distinct effects on soil bacteria and fungi populations and/or activity; on the other hand, the identity of the PGPR determines the performance of AM fungi (Medina et al. 2003). Thus, mycorrhizal effects depend on mycorrhiza helper bacteria and likewise the non-pathogenicity of *Fusarium* spp. depends on associations with ectosymbiotic bacteria as mentioned before. Mycorrhizal fungi, other fungi and PGPR may interfere with each other when it comes to plant signalling. All these links between plants, fungi, other fungi and PGPR necessitate multidisciplinary research programmes, especially when application is the aim of the research. Consortia of mycorrhizal fungi and PGPR have been successfully applied in reclamation programs of desertified and/or heavy metal contaminated soil (Azcón et al. 2013). Similarly, combinations of plant beneficial microorganisms can be applied in biocontrol strategies, for instance, *Glomus mosseae* and *Fusarium equiseti* has been shown to have an additive effect on control of anthracnose disease in cucumber (Saldajeno and Hyakumachi 2011). The detailed knowledge available for some PGPR needs to be placed in an ecological context to guarantee successful application (Hol et al. 2013).

3.5 Concluding Thoughts and Summary

When we compare the contributions of the different groups of microbes, there are many similarities in the way fungi and bacteria improve plant nutrition and relieve (a)-biotic stress. There is substantial knowledge on the potential mechanisms, but it often remains unclear what happens in nature. The ecological knowledge needs to match the physiological knowledge in order to know the role of mycorrhizal fungi in natural ecosystems or to improve the performance of PGPR. Compared to mycorrhizal fungi, the role of other fungi and PGPR in natural systems for plant succession or community dynamics is somewhat unexplored (but see Ahn et al. 2007). PGPR might play a bigger role in natural systems than thus far realized, but it has not been addressed as such. Indirectly, PGPR must have large impacts on species richness when revegetation success is increased by PGPR inoculation (Valdenegro et al. 2001). Thus although the individual PGPR in natural systems have not received the attention they might deserve, the awareness is there that microbes are crucial in determining a plant's ability to cope with the (new) environment (Callaway et al. 2004; Reinhart and Callaway 2006). A cross pollination of PGPR research and plant soil feedback could benefit both, with natural systems as models for sustainable biocontrol (Van der Putten et al. 2006). The applied PGPR research might benefit from the community perspective while the plant soil feedback in natural systems can explore the space that PGPR occupy in the black box of plant soil interactions (Cortois and de Deyn 2012). In terms of techniques the developments in molecular biology and isotope labelling enable rapid progress in revealing the contribution of individual species to community function. In terms of application it will be interesting to see whether we move towards integrating and stimulating natural beneficial

organisms in the rhizosphere or rather towards engineered crop species which incorporate desirable genes from their former mutualists. In the end it is the context which determines where the plant-microbe relation ends on the continuum between mutualism and parasitism. Understanding of the context will be facilitated by the fast technical developments which enable large scale studies under field conditions.

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Chapter 4

The Positive Effects of Trophic Interactions in Soil

Jennifer Adams Krumins

Abstract The feedbacks between plants and their soil communities determine primary production and moderates the ecosystem services they both provide. Feedbacks can be perceived as positive or negative, but historically, the greatest attention has been given to the role of negative feedbacks in shaping plant production and community development. Although we understand the role of mycorrhizae and bacterial symbionts fairly well, fewer studies have addressed the role of positive feedbacks and facilitation associated with trophic interactions and food web activity. Due to the close spatial scale of rhizosphere food webs, they function more like a cycle than a linear food chain. This results in consumer mediated nutrient cycling that frequently feeds back positively on plant production even when considering herbivory as an isolated process. Herbivores enrich the environment by increasing organic matter and high quality mineral nutrients to the soil. A process mediated by the stoichiometric imbalance between consumers and resources. Likewise, the functional and taxonomic biodiversity of food webs in soils will understandably affect the degree of positive feedbacks to plant production. This is important to consider in an increasingly human dominated world. It is possible that community composition and functioning in disturbed environments is driven to a greater degree by positive rather than negative feedbacks. In this environment, soils will play an essential role in maintaining ecosystem health.

4.1 Introduction

The complex community of organisms living in soil plays an essential role in the production and composition of the above-ground plant community. Likewise, primary production and plant community composition are the main contributors of

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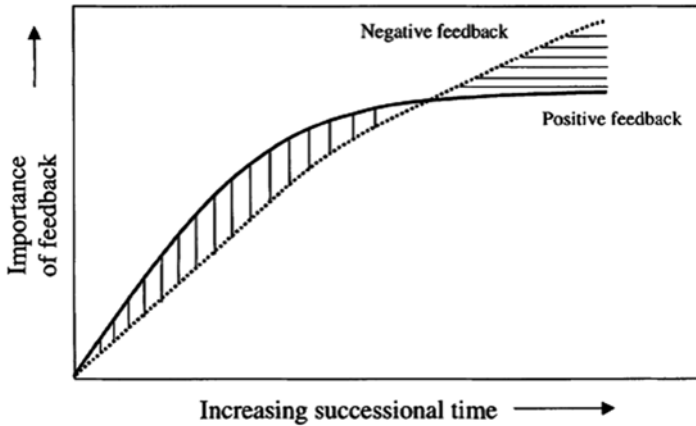


Fig. 4.1 The relative importance of positive and negative feedbacks from the soil as they influence plant community structure through successional time (The figure was adapted from Reynolds et al. (2003))

fixed carbon to belowground micro food webs fueling the ecosystem processes of soil. The term plant soil feedbacks is used to describe this bidirectional flow of interaction between plants above and soil matrix below (Bardgett et al. 2005; De Deyn et al. 2003; Krumins et al. 2013; Wardle et al. 2004). Feedbacks can be characterized as positive or negative to plant production (Wardle et al. 2004). The role of negative feedbacks in shaping plant communities has been studied for some time (e.g. van der Putten et al. 1993; Bever et al. 1997), but the role of positive feedbacks has been given far less attention. Reynolds et al. (2003) proposed the idea that succession and plant community development is not solely driven by negative below ground interactions (Fig. 4.1). They said that as a plant community develops through time, negative interactions eventually give way to positive interactions and facilitation in shaping aboveground plant community composition. As part of this, the positive feedbacks associated with mycorrhizal interactions will certainly increase as the plant soil relationship matures. In this chapter, I acknowledge but do not focus on mycorrhizae because they have been so well covered elsewhere (Allen et al. 2003; Dighton 2003) as well as Chap. 3 by Hol et al.). Rather, I would like to emphasize the positive feedbacks associated with trophic interactions and subsequent nutrient cycling.

At a fundamental level, how do trophic interactions in soil either directly or indirectly influence primary production and composition of the entire above ground community? This chapter addresses the benefits of consumption and soil food web activity to plant community production and structure. I begin by describing the cyclic nature of trophic control in soils. Due to the small spatial scale of soil food webs, the activity of consumers and predators contributes heavily to nutrient cycling and availability (Moore et al. 2003). Stoichiometry is central to making this process work because the difference between nutritional quality (the elemental ratio of C:N:P) of

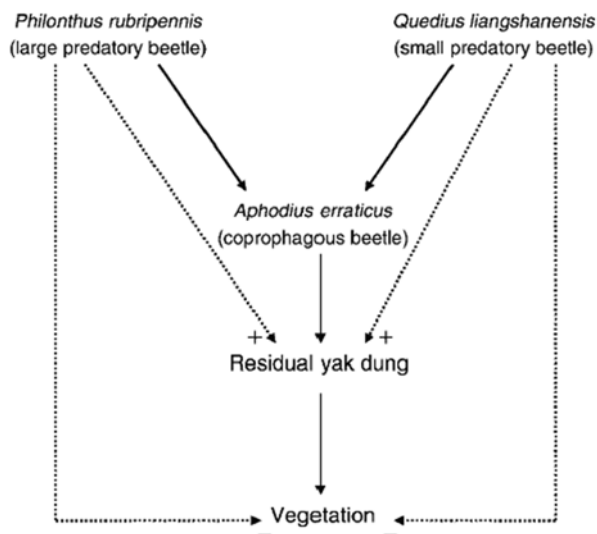
consumers and their resource can result in nutrient assimilation into biomass or release to the local soil environment (Sterner and Elser 2002). I then go on to highlight the paradoxically beneficial role of herbivores in plant production. The idea that herbivory is beneficial to plants has been theorized and researched. I review this research and propose hypothesized mechanisms to explain the phenomena. I conclude the chapter with a discussion of multi-trophic biodiversity in soils and its influence on plant production and community structure. Research has shown that more complex and diverse communities lead to greater ecosystem productivity and functioning. I will highlight the role of biodiversity in soils and the plant community, and how they may feedback positively on each other. Finally, I will look to future research and the notion that positive interactions may be increasingly important as the impacts of human activity on the soil grow.

4.2 Cyclic Nature of Food Webs in Soils

The conventional assumption that trophic control within an ecosystem is subject to either top-down predatory control (trophic cascades) or bottom-up (donor) control is not the most useful descriptor for soil food webs, especially in the rhizosphere. Rather, the transfer of energy, materials and nutrients through soil food webs has been described as a cycle (Moore et al. 2003) instead of the unidirectional designations given to describe aquatic food webs (Chase 2000). What we mean by this is that nutrients excreted by consumers serve as the basal resource for producers. Therefore the amount of consumption determines the amounts of mineral nutrients available and limits on primary production. In principle this is the case for all food webs (consider the microbial loop well described in aquatic environments (Azam et al. 1983)), but the designation of a cycle fits well in soils because of the decreased scale over which trophic interactions occur (Krumins et al. 2013).

In contrast to soils, in above ground or in aquatic ecosystems, fluid and organisms move more freely and over greater distance than they do in the often microscopic scale of soil aggregates in below ground ecosystems. In soils, mineral nutrients excreted by herbivores, primary consumers and predators frequently remain localized, taken up by nearby plants to further primary production (de Ruiter et al. 1993). The cyclic nature of soil food webs and trophic interactions leads to positive feedbacks for primary production through increased nutrient availability in the rhizosphere. This idea led Moore and colleagues (2003) to describe top-down trophic control in soils (grazing on fauna and microbial communities) as effectively bottom-up with respect to the plants (increased mineralization and nutrient availability to plant roots). This occurs through two mechanisms. First, in the classical sense, predatory control on herbivores can release plants from grazing pressure *sensu* (Preisser 2003), and second, mineral waste from all consumption provides the basal resources for plant growth and subsequent plant community dynamics. Recent interesting work illustrates where these two mechanisms can converge. Wu et al. (2011) describe a food web in which predatory control of coprophagic (dung eating) beetles slowed

Fig. 4.2 The decomposer food web studied by Wu et al. (2011), in which predatory beetles regulate the decomposition of yak dung by coprophagic beetles. Decomposition of dung has direct effects on nutrient availability to vegetation. *Solid arrows* indicate direct interactions, and *dotted arrows* indicate indirect effects



dung decomposition and further release of those nutrients to the soil and plants (Fig. 4.2). Their results show a surprising interaction when temperature caused warmed dung to decompose more slowly, resulting in reduced mineral nutrient availability in the soil. They explain this result by water loss from the warmed dung negatively impacting the coprophagic beetles.

The role of consumers in resource supply as well as trophic control has important implications for primary production and ultimately plant community diversity (De Deyn et al. 2003). Ecologists typically think of the biomass and community composition of soil fungi being determined by resource availability and bottom up affects. However, classic work has shown a shift in composition and subsequent decomposition by basidiomycete fungal communities associated with collembolan grazing (Newell 1984). Likewise, Crowther et al. (2011) recently showed that the composition of a decomposing fungal community in soil was controlled by invertebrate isopod grazers. The work by Crowther et al. was carried out in microcosms, but the outcome has important implications for decomposition and nutrient mineralization in all soils. Their work represents a case where top down control by a consumer is regulating decomposer community composition and the availability of nutrients in the soil with feedbacks to the plant community.

Ecological stoichiometry is the fundamental mechanism allowing consumer mediated nutrient cycling to take place (Sterner and Elser 2002). All organisms can be described by their elemental composition, and the relative amounts of these elements (carbon:nitrogen:phosphorus etc.) have implications for their metabolism and interactions with other organisms. Bacteria have a low C:N:P ratio while their consumers tend to have relatively higher C:N:P ratio. Generally, when consumers eat a resource that is of lower stoichiometric ratio they contribute mineral nutrients

to the soil. This is the mechanism behind the microbial loop, the feeding pathway between bacteria and their protist or nematode consumers that enriches the soil (Clarholm 1994). Conversely, when they consume something relatively depleted in mineral nutrients (a higher C:N:P), they contribute organic carbon to the soil (Osler and Sommerkorn 2007). This principle has been illustrated in research by Manzoni et al. (2008) in which they analyzed soil decomposition data from around the globe. They quantified microbial decomposition rates and carbon use efficiency relative to the detrital nitrogen content. They found that nitrogen content of the detritus impacted the fate of carbon and nitrogen to be immobilized, assimilated or respired. Specifically, they show that when decomposing consumers are nitrogen limited, the efficiency with which they assimilate carbon goes down, and carbon respiration goes up. Their meta-analysis presents this result as a global pattern insensitive to climate and geography. A logical extension of this work would be to consider decomposition carried out predominantly by fungi or bacteria. Fungi have a higher demand for carbon, and likewise their efficiency with carbon is greater than that of bacteria (Keiblinger et al. 2010). Together, these facts have important implications for global carbon storage, whether or not a soil is dominated by bacteria or fungi and the stoichiometric nutrient content of plant detritus (Hessen et al. 2004).

Stoichiometric quality of resources will affect the functioning of trophic control in soils. As one moves up through trophic levels, grazing on rhizosphere bacteria by protozoa and bacterivorous nematodes in the microbial loop results in a release of mineral nutrients to the soil that can further support plant growth (Bonkowski et al. 2009; Brussaard 1998). Plants pay for this stimulation of microbial metabolism by releasing their own fixed carbon, but the mechanism of nutrient mineralization and positive feedback to the plant is in the stoichiometric mismatch between the bacteria and the consumers in the microbial loop (Osler and Sommerkorn 2007). Protozoan grazers in the rhizosphere further influence plant production when they selectively graze particular bacterial taxa affecting the production of plant hormones by bacterial symbionts (Bonkowski and Brandt 2002) including production of indole acetic acid (Jiang et al. 2012).

The rate at which consumer excreted nutrients are recycled back to primary producers is determined by the C:N:P of those consumers. This is true in all environments, but it is especially so in soils and on land where nutritional quality of primary producers is relatively lower due to the structural constraints (lignin composition) of living with gravity (Sterner and Elser 2002). Indeed, primary producers in soil support slower nutrient cycling by their own consumers (Cebrian 2009). In spite of the fact that decomposer stoichiometry and enzymatic activity remain fairly constant across all habitats (Sinsabaugh et al. 2009), plants rooted in soil and their supported consumers (Osler and Sommerkorn 2007) are limited in their capacity to cycle nutrients and produce biomass by their own elemental composition. At a very basic level, soils are unique in that the cyclic nature of their nutrient turnover is very short in temporal and spatial scale, but because of the constraints of being on land the process will always be limited by the elemental composition of the primary producers.

4.3 The Paradox of Herbivory

Though the focus of this chapter and entire volume is feedbacks to the plant from soil, it is challenging to separate the effects to the plant of herbivory in the rhizosphere from that occurring above ground in the stems and leaves (Bardgett and Wardle 2010; Wardle et al. 2004; Gough et al. 2012). Herbivory above ground or below can have a profound effect on the other with respect to plant herbivore defenses (Bezemer and van Dam 2005) as well as carbon allocation (Bardgett et al. 1998) and the composition of the micro-fauna food web and community (Veen et al. 2010). When herbivores consume plant biomass, either aboveground or below, they release mineralized nutrients into the environment that support microbial activity and further primary production (Bardgett and Wardle 2003; Hamilton and Frank 2001; Ruess and McNaughton 1987; Yeates et al. 1999). The increase in primary production can occur through two non-mutually exclusive mechanisms. First, plants may ‘over yield’ and compensate for herbivory with additional growth (Agrawal 2000). Second, due to a stoichiometric imbalance between the herbivore and the plant, a herbivore may excrete excess mineral nutrients into the surrounding environment (Cherif and Loreau 2013). The degree to which herbivore mediated enrichment takes place is likely determined by the stoichiometric imbalance between the consumer and the consumed and the efficiency with which the consumer eats. Indeed we see that when herbivory is not too intense, it can stimulate the microbial community in the soil and plant growth (Denton 1999) analogous to results seen when fungal biomass increases under light grazing (Lussenhop 1992). Even on un-grazed roots, bacteria accumulate in the rhizosphere to capitalize on root exudates and labile carbon. When roots are grazed, microbes have more to gain when herbivory leaks more carbon into the soil (Yeates et al. 1999).

4.3.1 *Herbivore Efficiency*

Herbivores can be inefficient consumers. As they graze, leaf material above ground or root exudates and particles below ground are not completely ingested (Anderson et al. 1985), and this non-ingested plant material primes the soil, feeding microbial metabolism (Bardgett and Wardle 2003; Hamilton and Frank 2001; Mikola et al. 2009; Kuzyakov et al. 2000). The mechanism of inefficient consumption priming the soil is dependent on the principles of ecological stoichiometry. Whether or not the excess organic matter is ingested, decomposed and mineralized by the herbivore or microbes depends on the efficiency with which the herbivore ingests the plant material. Following that, the stoichiometric imbalance between plant material and the microbial or herbivore pools will determine whether organic carbon accumulates or mineral nitrogen accumulates in the soil. These facts determine whether or not the plant will benefit from the priming effects (Kuzyakov et al. 2000) of an inefficient herbivore or suffer from the consumptive effects of an efficient herbivore.

This principle holds for both above-ground and below-ground herbivory, but the benefits are all realized below-ground in the rhizosphere where nutrient absorption takes place.

The efficiency with which a herbivore grazes may determine the degree of positive or negative feedback to the plant. Conventional wisdom would say that organic material released in the course of herbivory imposes a direct cost to the plant. However, when herbivores are inefficient, not all plant material grazed translates into increased herbivore biomass and fecundity; some is lost to the detrital pool through ‘sloppy eating’. The left-overs of sloppy eating increase the abundance of fine particulate organic material with greater surface area and capacity for microbial decomposition and mineralization. Further, the ability of a herbivore to live, die and consume may be affected by pathogens and predators. Recent work has shown that microbial pathogens, acting in some ways as predators, in soil can control herbivorous nematode populations (Piskiewicz et al. 2007) and thus affect the efficiency and intensity of herbivory.

Earlier and extensive work has set the foundation for herbivory theory in above-ground communities (McNaughton 1976) that has been tested below ground much less. Past work has shown that that roots below ground can over yield in the same way above ground biomass can, because increased root biomass was found in grazed as opposed to un-grazed roots (Bardgett et al. 1999). However, no one yet has considered that this may not be purely a plant physiological response. Instead, the mechanism behind this effect is likely explained by metabolic processes in the soil. In one experiment, when nematodes grazed roots, organic nutrients were released and microbial nitrogen cycling increased (Tu et al. 2003). The degree to which organic nutrients are released to the soil, the stoichiometric quality of those nutrients and the selective grazing of the herbivore will determine if they are digested by the herbivore or decomposed and mineralized by microbial consumers and ultimately any benefit to the plant (Bardgett and Wardle 2003).

4.4 Multi-trophic Biodiversity of Soils Supporting Plant Communities

4.4.1 What We Know About Soil Biodiversity

Ecological theory has primarily accepted the notion that ecosystem functioning increases with greater species richness (Duffy et al. 2007), though the discussion continues (Wardle and Jonsson 2010). In fact, extensive work in recent decades supports this notion with an increasing emphasis on studies that consider whole food web and multitrophic diversity. The importance of soil food web diversity and its likely positive feedbacks to primary production are timely and critical. In recent years, the contribution of soil communities and specifically soil food webs to global biodiversity and ecosystem functioning has been brought to the forefront of

biodiversity research (Wall et al. 2010; Coleman and Whitman 2005). Soils are likely the most biodiverse realm on earth, and they support ecosystem functions critical to life on earth (Bardgett and Wardle 2010; Wall 2004; Coleman and Whitman 2005). However, organisms in soil are dependent upon primary production from the sunlit portion of the world to supply needed fixed carbon. As is one of the central themes of this volume and chapter, plants above ground and soil communities below are in a constant and dynamic exchange between each other. The diversity and likewise functioning of the organisms in the soil plays a central role in those feedbacks and primary production.

4.4.2 How Soil Diversity Can Support Primary Production

A seminal paper published by Hol and colleagues (2010) demonstrated that rare microorganisms, as opposed to those most abundant in soil, increase plant yield in model agricultural systems. They found this through a series of serial dilution experiments where pots were inoculated with successively less diverse microbial communities. The diversity of the initial inoculum was realistically un-even allowing the researchers to study the importance of rare taxa. This finding was very important to shed light on a longstanding debate within the biodiversity literature (Hooper et al. 2005): do more diverse communities function better because there is an increased likelihood of there being a functionally dominant organism? The work of Hol et al. (2010) was limited to microbial taxa, but extending this question to entire micro-food webs within the soil would be enlightening. Indeed studies have shown that fungivory by soil micro-arthropods and nematodes altered the composition of saprotrophic fungi and their capacity to decompose and cycle nutrients in the rhizosphere (Crowther et al. 2012; Newell 1984). The diversity of the decomposers had a direct affect on the functioning of the fungi similar to that seen in other studies of microbial decomposition and plant diversity (Miki et al. 2010). This complements other research findings showing that diversity of ectomycorrhiza, regardless of the taxa present, affects host plant production (Baxter and Dighton 2001) and that decomposer diversity and presence significantly affects above ground plant community composition and functioning (Eisenhauer et al. 2012). These results make sense in light of the fact that the ecosystem functioning of decomposers is central to the availability of mineral nutrients in the soil and therefore, plant production. More studies testing multitrophic and whole food web diversity will reveal interactions between diversity and the indirect effects of cyclic trophic control in soils. Globally, there is so little soil that has not been impacted by human activity (Pickett et al. 2011). The biodiversity of these soils may influence the degree to which humans can count on them for ecosystem services. Indeed, this is an important and growing area of ecological research, whether or not degraded and urban soils can still carry out the ecosystem functions on which we depend (Grimm et al. 2000 and see Chap. 10).

4.5 Discussion and a View to Future Research

Because so much of soil functioning and community dynamics occur at the micro-scale, they are especially challenging to study. This leaves large gaps in our knowledge base right at a time when our understanding of the services carried out by soils is most critical. The role of facilitation and positive feedbacks is receiving more and more research attention. To conclude this chapter, I want to challenge the notion that negative feedbacks from the soil predominantly drive plant production and community composition. Likewise, facilitation is not limited to the beneficial influences of mycorrhizal relationships or nitrogen fixing bacteria. Positive feedbacks to plant communities are realized through trophic interactions and subsequent nutrient cycling. An increased diversity of taxa within those food webs will likely result in positive feedbacks to plants through a couple of mechanisms: an increase in nutrient enrichment for primary production or a decrease in the ability of pathogens to invade a more diverse rhizosphere community.

Appreciation for the role of positive feedbacks on primary production and plant community structure is growing (Bruno et al. 2003). This is important because in reality, there is likely a dynamic interplay between positive and negative feedbacks that constantly influences the fate of the plant community. Thus far, most of the attention paid to positive feedbacks from soil has been with respect to plant invasions (Callaway et al. 2011). However, as we start to understand increasingly human dominated landscapes, positive feedbacks may be seen to take on a more important role to entire plant communities, not only the exotic or range expanding species. The indirect nutrient enrichment associated with trophic activity in the rhizosphere or beneficial mutualists like mycorrhizae may facilitate plant community development on soils that would otherwise be restrictive to plant growth. Indeed we have seen urban brownfields, impacted by years of industrial and railroad activity, regenerate vibrant and diverse plant (Gallagher et al. 2011) and animal communities (Hofer et al. 2010) in spite of heavy soil contamination from metals and organic pollutants. The adage that ‘the forest returns’ is true, and this truth may be explained by facilitation from the soil.

The benefits of mycorrhizal associations may go well beyond their famous role as symbionts when they interact with fungal grazers and other micro food web participants. We now know that the presence of fungal hyphae in soil can be quite ephemeral (Allen and Kitajima 2013), but to what degree is this due to a shift in resource allocation by the fungi or interactions with fungivorous consumers? Is this process different for purely saprotrophic fungi or mycorrhizal fungi? Mycorrhizal fungi can compete with plant parasitic nematodes for access to roots (Hol and Cook 2005), possibly influencing this interaction or that with the root. Another potentially important yet little studied positive feedback in soil is that of the role of phage (See Chap. 8 by Reavy et al. for further discussion of this topic). In ocean sediments, the ‘viral shunt’ has been much studied as a critical path for nutrient cycling and production (Danovaro et al. 2008). In this theory, bacterial lysis by phage releases limited nutrients and furthers bacterial production. This process occurs in the depth

of the ocean where plant growth will not occur, but the process may be much the same in soils. That is, nutrient release through phage induced bacterial lysis increases nutrient availability and stimulates further microbial but also, plant production. Though we know more about the viral influence in soils (aside from that known on agricultural pathogens) (Fierer et al. 2007), their functional role and possible positive feedbacks to plants are less well known.

Theory and conventional wisdom states that negative feedbacks from the soil diversify plant communities, while positive feedbacks homogenize them (Reynolds et al. 2003; van der Putten et al. 2013; Terborgh 2012). In fact, recent research testing the role of plant-soil feedbacks in shaping biodiversity demonstrated that overyielding associated with more diverse communities may not only be the result of niche complementarity but rather may also be caused by a dilution in realized negative feedbacks when more species are present (Maron et al. 2011; Schnitzer et al. 2011). This supports the notion that negative feedbacks drive plant community structure and coexistence of species. The homogenizing effect of positive feedbacks is in part explained by mycorrhizal associations. Mycorrhizal diversity is closely linked to plant diversity (van der Heijden et al. 1998, 2008), but also, mycorrhizal networks (Simard et al. 1997) and plant communication (Bais et al. 2004) connect plant species below ground such that interspecific competition for resources in the rhizosphere may be lessened. Recent theory challenges the notion that negative feedbacks alone drive biodiversity (Revilla et al. 2013), and it supports the idea that context and temporal dynamics may influence when positive or negative feedbacks control species coexistence. In a world where biodiversity is vulnerable, the role of indirect nutrient enrichment and facilitation associated with greater species diversity across trophic levels needs more attention. This is especially the case in soils where so many critical ecosystem functions take place. Finally, positive feedbacks and facilitation from soil organisms must ultimately dominate or balance the negative feedbacks or plants would not allocate so much of their resources to the roots (and soil through leaked carbon). The mechanisms behind these kinds of facilitation are so interesting yet challenging to resolve and in need of more research attention.

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Chapter 5

Soils Suppressing Biodiversity

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Abstract Soil biodiversity has been shown essential to provide ecosystem services for plant growth that have large economic value. However a number of ecosystem management practices and the effects of pollutants can decrease soil biodiversity and, hence, reduce its role in sustaining plant growth. This chapter briefly explores the diversity of soil organisms and the effects of pollutants on this diversity and concentrates on the management of agricultural ecosystems that minimize our impacts on soil diversity and function. Specific examples have been selected from viticulture, organic row crop agriculture, grassland farming and agroforestry. It is concluded that we need to understand more the role of biodiversity in soils and how we affect it with our agricultural practices and foresee a need for broader education in and awareness of soil ecology to improve management decisions in agriculture and land use management.

5.1 Introduction

Soil biodiversity is recognized both by the Convention on Biological Diversity (CBD; URL: <http://www.cbd.int>) and by the European Commission in the thematic strategy for soil protection (European Commission COM 2006) as essential for ecosystem functioning. In parallel, the Millennium Ecosystem Assessment (MEA 2005), has underlined the strong relationships existing between biodiversity and ecosystem services defined as “the benefits provided by ecosystems to humankind as well as

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other species". In fact, many ecosystem services are provided by multiple species (Jax 2005; Lavelle et al. 2006). In consequence, human well-being, which is based on these services, is strongly linked to this biodiversity. The cost of inaction with regard to the loss of biodiversity has been evaluated to be equivalent to 50 billion per year (1 % of world gross domestic product) and could reach 14 billion in 2050 (7 % of world gross domestic product) (Braat and ten Brink 2008). Therefore, humans all have an interest in taking care of biodiversity, and to develop tools i.e. indicators to be aware of the decline in biodiversity, its maintenance or its improvement in degraded situations.

Soil biodiversity is thought to harbor a large part of the world's biodiversity (Gardi et al. 2009). The relationships between biodiversity, aggregate ecosystem functions and ecosystem services have been identified, and revealed the huge impact for human well-being (Kibblewhite et al. 2008). However, this soil biota is assumed to have decreased, and the Thematic Strategy for the Protection of Soil adopted by the European Commission in September 2006 has identified loss of soil biodiversity as a soil degradation process. It is now recognized that this loss of biodiversity is strongly related to human activity, such as agriculture, industry, urbanization. However, due to the increase of human populations, the pressure on soil biodiversity may continue to increase in the future. It is therefore necessary to be aware of how industrial activity, which could generate pollution (metallic and organic pollution), or agricultural practices impact on soil biodiversity, its functions and therefore soil ecosystem services. This knowledge should assist stakeholders in the choice of sustainable management practices in industry, in agriculture and in natural ecosystems (Pulleman et al. 2012).

5.2 Soil Biodiversity Below and Above Ground

Soil biodiversity comprises 'the variation in soil life, from genes to communities, and the ecological complexes of which they are part, that is from soil microhabitats to landscapes' (Turbé et al. 2010). This variation is generally described in terms of three interrelated attributes of biodiversity: composition, structure and function (Noss 1990). Soil organism probably represent as much as 25 % of the 1.5 million described living species world-wide (Brussaard 1997; Decaëns et al. 2008). This represents as much as five times the known biodiversity of a forest canopy (Stork 1988; May 1990). Despite their significant contribution to global biodiversity, our taxonomic knowledge of soil biota is still poor compared with that of most aboveground organisms and less than 10 % of the species have been described. This knowledge should improve in the next decades thanks to new tools such as biomolecular tools (Decaëns 2010).

Soil organism density can be quite high: fauna represent several million m^{-2} which corresponds to several tons ha^{-1} (Bachelier 1978; Gobat et al. 2003; Lavelle and Spain 2001). As an example, a pasture under temperate climate can host 260 individuals per square meter (Gobat et al. 2003) which represent 1.5 tons ha^{-1} ; the

Table 5.1 Abundance (number m^{-2}), biomass (g m^{-2} for fauna, $\mu\text{g g}^{-1}$ for microorganisms) and species richness of soil biota from temperate regions

Group	Abundance	Biomass	Number of species
Bacteria	10^{12} – 10^{14}	100–700	4,000 genotypes
Fungi	10^9 – 10^{12}	100–500	2,000
Algae	10^6 – 10^9	20–150	
Protozoa	10^5 – 10^{11}	6–>30	68
Nematode	10^4 – $3 \cdot 10^6$	1–30	65
Acari	2×10^4 – 4×10^5	0.2–4	140
Collembola	2×10^4 – 4×10^5	0.2–4	48
Insect larvae	ca. 500	4.5	>245
Millipedes	20–700	0.5–12.5	6
Isopods	ca. 1,800	ca. 4	6
Earthworms	50–400	20–400	11 (+ 36 enchytraeides)
Permanent pasture, temperate context			Beech Forest in Europe

From, Torsvick et al. (1994), Schaefer et Schauermaann (1990), Hawksworth (2001), Gobat et al. (2003), Cluzeau et al. (2012)

equivalence of the weight of two cows, or six sheep. The biomass is much higher, when it also takes into account the microflora (bacteria and fungi) reaching 4.5 tons ha^{-1} .

Under forest soil, more than seven million invertebrates can be observed under the foot of a hiker, corresponding to 1,000 species per square meter (Schaefer et Schauermaann 1990). Arthropods are mainly composed by Mites (Acarina) and springtails (Collembola) (from 75 to 80 % of the total number). Focusing on fungi density, the mycelium represents several kilometers in the soil; 1 cm^3 of mycelium corresponds about 40 km of hyphae, and therefore in forest there are more than 200 km of hyphae per 1 m^{-2} . A single gram of forest soil may also contain as many as 4,000 genotypes of bacteria and about 2,000 species of fungi (Torsvick et al. 1994; Hawksworth 2001) (Table 5.1).

Soil organisms are mainly located in the top 0–30 cm of soil where soil resources and nutrients are consistent (organic matter content), as well as porosity and moisture. However, soil organism show a strong vertical distribution, generally with increasing soil depth. Soil organism density decreases and, more than 88 % of total nematode population are observed in the top 0–10 cm (Yeates and Bongers 1999).

Soil organisms are very diverse in terms of size, color, morphology, life habitat, food resource, life strategies. They have been traditionally classified according to their body size, which reflects their adaptive strategies to habitat constraints (Lavelle and Spain 2001). According to different authors (Bachelier 1978; Bonneau and Souchier 1979; Lavelle and Spain 2001), microorganisms correspond to organisms whose size does not exceed 0.2 mm length; they belong to the microflora (Bacteria including some relevant group such as Cyanobacteria and actinomycetes, Archea, fungi, and alga) and microfauna (Protists, formerly known as Protozoa and nematodes); microfauna live and feed in the free water films and soil porosity; they are considered permanent soil dwellers; they are generally well adapted to occasional desiccation and/or shortage of food in their micro-environment; they

operate at spatial scale of a few millimeters (at the soil aggregate scale). Protists are mostly heterotrophic, nonfilamentous, unicellular organisms, although some of them (Euglenida) includes species that possess chloroplasts. There are at least 50,000 name species of protists. They occupy the spore space outside the microaggregates and their growth rates have been reported to decrease when soil compaction increases (Couteux 1985). Moreover, they are dependent on the presence of liquid water in soil and therefore their activity ceases when soil becomes to dry or when soil salinity exceeds 25 % sodium content (Whalen and Sampedro 2010).

Mesofauna have a body size from 0.1 to 2 mm and include tardigrades, microarthropods (Collembola, mites-Acarina) and Enchytraeidae (Oligochaeta); they depend on high moisture levels (some of them require free water in their environment); they move freely in the pore space (on soil surface in the litter or in soil) and the spatial scale at which they operate is that of from 5 to 20 cm. Macrofauna have body size from 2 to 80 mm; they include earthworms (large Oligochaeta), mollusks and Arthropods (Isopoda, Myriapoda, Araneida, Opilionida, termites, ants); some of them live on the soil surface; others can dig burrows in the soil and, due to their body size, redistribute soil porosity. They operate at spatial scale of from 50 cm to 5 m (earthworms can dig burrows which reach 5 m depth). This size limit between mesofauna and macrofauna could move from 2 to 4 mm depending on the authors (Gobat et al. 2003). Megafauna have body size from 80 to 160 mm, they mainly include vertebrates such as moles and voles; in fact they are rarely included in soil biodiversity assessments because of their low density (Pulleman et al. 2012).

Classification of soil organisms can also be based on the time soil organisms spend belowground, i.e. for their life cycle. Geobiont species represent soil organisms who spend all of their life cycle, from larvae to adult growth stage, belowground; it is the case of earthworms, nematodes, protozoa, mites and collembola. Active geophil species correspond to soil organisms that spend part of their life cycle (larvae) belowground, such as Diptera and Coleoptera larvae. Inactive geophil species limit the use of soil as a refuge to be protected from climate constraints (Gobat et al. 2003).

Soil organisms may also be classified in terms of morphological characteristics which are related to the nutritional resource they use and their microhabitats. Indeed, a vertical stratification of soil organisms could be observed related to their morphological adaptation to endogeic life (Bouché 1972; El Titi 2003; Gobat et al. 2003; Jeffery et al. 2010). From soil surface to depth, soil invertebrates present a reduction of the appendices length (legs, antenna), they are flatter and longer while species living on soil surface are shorter and more round. A reduction of the optic organ is observed as well as a decrease of the body pigmentation to the point of non-pigmentation (endogeic earthworms are white or poorly colored) while organisms living on the soil surface are pigmented. Taking into account that life forms always deal with energetic balance, the reason why organism who live on soil surface are pigmented is related to the benefits gained by putting energy for pigmenting their integument: they protect them self from sun rays (UV protection) (El Titi 2003) and by mimicking their environment, they decrease the risk of predation (Bachelier 1978). This vertical stratification distinguishes different biological taxa,

Table 5.2 Relation between the classification based on body size and functional classification

Size classes	Functions	Functional groups
Microorganisms	Decomposition of organic matter, release of elements, nitrogen fixation, regulation of some pathogens	Chemical engineers
Microfauna	Regulation of microorganisms through predation, can be parasite of plants or animals	Biological regulators, microbivores or micropredator
Mesofauna	Fragmentation of organic matter can be predators of microfauna	Detritivors or litter transformers
Macrofauna	Fragmentation of organic matter, modification of soil structure, some are predators	Ecosystem engineers

e.g. micro-arthropods are living on soil surface while some earthworm species are living at 30 cm deep in soil. Moreover, this vertical stratification also distinguishes functional groups within a biological group. Within Collembola, springtails such as Entomobryidae or Sminthuridae live in the leaf litter and at the soil surface (epigeal or surface-living Collembola), they are pigmented, with well-developed furcula, strong legs, eye patches, long scales or hair to prevent desiccation; in contrast, euedaphic Collembola such as *Protaphorura sp.* live in deeper soil layers, are elongated hexapods with diminished eyes (or no eyes), reduced limbs, extremely reduced furcula and are lacking pigmentation (Jeffery et al. 2010; El Titi 2003). These criteria of body size, pigmentation, sclerotization and limb length is also applied to mites, and dipteran larvae (El Titi 2003). Similarly, criteria of body size and pigmentation are also applied to earthworm species and lead to the definition of three ecological groups (Bouché 1972). Epigeic earthworm species who are small (5 cm length at adult stage) and highly colored (red, black) live at soil surface in organic matter; endogeic species who are longer (5–20 cm length) and poorly pigmented (white, red) always live in soil, while anecic species who are much longer (5–110 cm in temperate conditions), presenting a gradient of color from the head to the tail (head is brown-black or red, and tail is light), live in soil but reach soil surface for feeding. All of these specific features of soil invertebrates express the robustness of the taxa involved to live in a given soil environment (Lavelle and Spain 2001).

5.2.1 Soil Biodiversity and Soil Properties

The impact of soil organisms on soil properties and soil functions is strongly related to the body size of these organisms (Table 5.2). Microorganisms, e.g. bacteria, fungi and algae, are the main drivers of organic matter decomposition, nutrient transformations and degradation of toxic compounds (Pulleman et al. 2012). These decomposers and nutrient transformers are grouped as “chemical engineers” (Kibblewhite et al. 2008; Turbé et al. 2010). Microfauna (nematodes) and mesofauna (collembolan) act as herbivores or predate on other invertebrates or micro-organisms; these ‘Biocontrollers’ or ‘biological regulators’, through predation, regulate the activities

of the microbial community and thereby releasing nutrients (Didden et al. 1994). Soil macrofauna act on soil through physical actions (creation of burrows, chamber, production of casts deposit on soil surface or in soil), and also chemical actions (ingesting organic matter and mixing with soil) (Blouin et al. 2013). Therefore, they can modify the soil habitat in terms of physical structure and availability of resources to other soil organisms, and they have been characterized as ‘ecosystem engineers’ (Jones et al. 1994).

5.3 Biodiversity and Contaminated Soils

Pollutions linked to anthropic activities from agriculture, industry or urbanization, create a stress which often leads to an imbalance of ecosystem. In the case of soil pollution, organisms are exposed to different fractions of pollutants, either by contact (e.g. dissolved in soil solution) or by ingestion (sorbed on soil components) (Hedde et al. 2012). Contamination can impact soil organisms at different levels, from cellular to community levels (Corted et al. 2000).

In the case of metallic contamination, the high quantity of contaminant in soil, such as mercury or zinc impacts the microflora community by decreasing the density of the population (Müller et al. 2001), the bacterial diversity (Moffett et al. 2003) and microbial activity such as phenol oxidase (Floch et al. 2009). These effects lead to the decrease of mineralisation which induces litter accumulation and high organic matter content in very contaminated soils (Cotrufo et al. 1995). Metallic contamination also impacts soil invertebrates. At infra-cellular level, an increase in proteins and the number of transcripts coding metallothionein is observed when earthworms are exposed to metallic contamination, especially Cd (Morgan et al. 2004; Brulle et al. 2006; Demuynck et al. 2007; Pérès et al. 2011). At a cellular level, an alteration of collembolan midgut cells is observable (Pawert et al. 1996). At an individual level, the decrease of larval development and fertility of Carabidea have been demonstrated (Mozdzer et al. 2003; Lagisz et al. 2002). At population or community level, metallic contamination decreases earthworm abundance (Pizl and Josen 1995; Spurgeon and Hopkins 1999; Lukkari et al. 2004), species richness (Nahmani and Lavelle 2002) with a strong negative impact on endogeic species (Pérès et al. 2011).

Despite the fact that in many research studies, a strong relationship has been observed between the gradient of contamination and the soil biological state, some contrasted results are noticed in the literature, underling the complexity of the interactions in soil. In fact, the impact of contamination appears to be strongly related to the bioavailability of contaminant contents rather than total contents, and this bioavailability is depending on soil physical and chemical properties such as pH, organic matter content and state (van Gestel 2008). Moreover, the impact of contaminant on soil biodiversity is also impacted by soil management: under low level of contamination, the soil agricultural management such as reduced tillage system could balance the negative effect of contaminant (Pérès et al. 2011).

5.4 Soil Biodiversity and Agriculture

Cultivable soils represent 30 % of emerged earth, which correspond to 4.2–4.4 billion ha; however only 12 % are really cultivated because there are many places covered by cold or hot desert, rocks or which have a significant slope (Griffon 2006). Biodiversity is strongly impacted by land use (e.g. forest, crop, pasture) and also agricultural practices (e.g. fertilisation, use of pesticides, tillage or no tillage system), therefore it is important to take into account these different levels of management in any analyses. A study conducted on 109 sites in France (Cluzeau et al. 2012) which studied most of soil organisms, revealed that the abundances of earthworms, nematodes, mites, bacterial community as well as microbial biomass and earthworm species richness were strongly impacted by land use (crops *vs.* meadows *vs.* forests) (Cluzeau et al. 2012; Villenave et al. 2013; Ponge et al. 2013). Macro-invertebrate abundance, collembolan abundance and richness, and nematode richness were only relevant for the discrimination of agricultural practices (e.g., management system or fertilisation intensity). Most of the soil biological groups (except collembolan) exhibited lower abundance and community richness in croplands than in meadows (Cluzeau et al. 2012).

5.4.1 Soil Tillage

Soil tillage is defined as mechanical or soil-stirring actions exerted on soil to modify soil conditions for the purpose of nurturing crops. The aim of these actions is to provide a suitable environment for seed germination and crop development while suppressing weeds and maintaining adequate soil moisture (Köller 2003). This practice has a long history and culminated in the invention of the well-known Roman plow. The technical evolution of tillage machinery combined with the evolution of chemical industry and use of pesticides was closely associated with a remarkable increase in crop production (Köller 2003). However, the world community has clearly acknowledged the negative aspects of agricultural expansion as the 1992 Rio Treaty was signed by 189 nations. Moreover, the intensive application of these practices, especially extensive deep plowing, also increase the risk of erosion can lead to catastrophic phenomena such as “Dust Bowl” in 1930 (Labreuche et al. 2007). In fact, plowing is often accompanied by the degradation of soil structure, leading to subsoil compaction, soil surface seals, erosion, and a decrease in soil organic matter (Friebe et al. 1991; McCarty et al. 1998; Holland 2004; Six et al. 2000). Seasonal ploughing can adversely affect soil quality, biodiversity, and productivity (Shaxson et al. 2008; Henle et al. 2008). In order to achieve the goal of safe productivity while protecting natural resources, ploughless “conservation tillage” (CST) and “no-tillage” (direct seeding, NT) management practises were developed in the USA, and initially applied in Europe in the 1950s with a visible extension since 1990. The impact of these reduced tillage systems have different impact on soil organisms.

5.4.1.1 Earthworms

In most of the research studies, reduced tillage systems increase the density and biomass of earthworms (Chan 2001; Ernst and Emmerling 2009; Pérès et al. 2010; Emmerling 2001; Peigné et al. 2009; Metzke et al. 2007; van Capelle et al. 2012; Roger-Estrade et al. 2010; Wardle 1995). It also increases the species richness and species diversity (Edwards and Lofty 1982; Holland 2004; Pelosi et al. 2009). Moreover, reduced tillage systems impact the functional diversity by changing the community composition of ecological groups and in many cases enhancing anecic species such as *Lumbricus terrestris* (Edwards and Lofty 1982; Kladivko 2001). These results, supported by the review from van Capelle et al. (2012) are explained by (i) an increase of organic matter on soil surface which provide a convenient food source (especially for epigeic and anecic worms), (ii) good conditions of soil moisture favorable to endogeic and anecic worms, (iii) non perturbation of soil limiting the body injury and the destruction of the burrows created by anecic worms, (iv) decreased exposure to predators at the soil surface. However, the favourable impact of reduced tillage system is moderated by soil texture: reduced tillage systems promote earthworm abundances in silty and loamy soils, while there is no positive impact in sandy soil (van Capelle et al. 2012). Furthermore, if results are constant for anecic species, results are more variable concerning the impact on endogeic species: conventional tillage by burring organic matter should be benefit to endogeic species (Nuutinen 1992; Pelosi et al. 2009). By promoting earthworm development, reduced tillage systems and especially direct-seeding systems, impact earthworm activity by enhancing the volume of burrows and the production of cast (Tebrügge and Düring 1999).

5.4.1.2 Collembola

Research studies document various tillage effects upon collembolan. Edwards and Lofty (1969), Sabatini et al. (1997), Petersen (2002) and El Titi (2003) reported higher density of collembolan in un-plowed systems, while the review of van Capelle et al. (2012) reported the decrease of collembolan density and species diversity due to the reduction of tillage intensity. These last results were supported by Loring et al. (1981) who suggested that both mold and chisel-plow tillage stimulate an increase of collembolan (and mites) population, presumably due to improvement of nutrient availability, pore space and other soil physical properties. The impact of reduced tillage systems seems to be closely related to the different groups: euedaphic species present a more stable population under non-inversion tillage; in contrast, plowing would reduce population of surface-dwelling collembolan most intensively due to the loss of shelter, surface crop or crop residues as protecting cover or food resource and changes of moisture conditions (El Titi 2003). However, the contrasted results obtained in the different studies could be explained by the complexity of interacting effects: tillage effects are life-strategy dependent (life-cycle, dispersal patterns), moreover collembola are differently affected by soil tillage intensity depending on the particle size distribution characterizing their habitat in association with their ability or inability to burrow (van Capelle et al. 2012).

5.4.1.3 Nematodes

Various tillage effects have been reported by research inventories. Reduced tillage systems can promote nematodes density and the diversity of the community (Villenave and Ba 2009; Parmelee and Alston 1986; Miura et al. 2008; Bouwman and Zwart 1994). This is explained by the organic matter on soil surface, the more suitable soil moisture conditions and the absence of mechanical perturbations. However, contrasted results have been showed by Fu et al. (2000) and Treonis et al. (2010) who described a decrease of nematode abundance, or the review of van Capelle et al. (2012) who showed no significant effect except for root-feeding species who took benefit from no-tillage system. In fact, many studies concluded that nematode responses to tillage intensity are highly variable and obviously depend on numerous other factors such as food sources, pollutant loads, pH, drought, management practices such as crop species (El Titi and Ipach 1989; El Titi 2003; Carter et al. 2009; McSorley and Gallaher 1994; LopezFando and Bello 1995; Holland 2004).

5.4.1.4 Microorganisms

The analyses of literature done by Andrade et al. (2003) who analyzed data from several studies in many parts of world under both temperate and tropical conditions, showed in general higher levels of microbial biomass under no-tillage than in conventional tillage systems. However, contradicting results from analyses of dataset done by van Capelle et al. (2012) showed that overall microbial biomass was not impacted by reduced tillage systems. These contrasted results could be explained by the climate and also the duration of the experiment, i.e. the positive impact of no-tillage systems increases with duration of the experiment (short-term vs. medium-term vs. long-term) (Andrade et al. 2003). The negative impact of tillage is primarily related to the disturbance of the soil environment after tillage, as well as the damage of the fungal network: fungal which have a greater biomass than bacteria are more adversely altered than bacteria (Whalen and Sampedro 2010). The positive impacts of reduced tillage systems are related to cropping and residue management practices: no-tillage systems retain more crop residues and, hence, sufficient substrate to sustain microbial community in higher levels. The management of crop residues and the tillage action also leads to a vertical distribution of microbial biomass in soil which differed significantly between tillage systems. Indeed, in reduced tillage systems soil microbial biomass (as well as mineralization of carbon and nitrogen) tend to be greater in the upper layers of the soil and decrease with depth, while they are more homogeneously distributed throughout a soil depth of 0–30 cm with a traditional mouldboard ploughing (Meyer et al. 1996; Young and Ritz 2000; Kladvko 2001; Vian et al. 2009). This vertical distribution is explained by organic matter availability, i.e. burying depth of crop residues, and also by soil structure, i.e. soil compaction (Vian et al. 2009). Focusing on the bacterial community, Vian et al. (2009) demonstrated that the bacterial community structure of the 0–7 cm soil layer differed markedly from the others soil layers, for both conventional plowing systems and reduced tillage systems.

Reduced tillage such as no-tillage system has been reported as a system that enhances microbial enzymatic activity (e.g. acid phosphatase, arylsulphatase, dehydrogenase, alkaline phosphatase, urease, protease), compared with conventional ploughing systems (Andrade et al. 2003). Indeed, reduced tillage systems, especially no-tillage systems, have the potential to benefit microbial communities occurring in the upper soil layer via improved quantities and qualities of food supply and thus, to promote the processes they drive, improving soil fertility and productivity (van Capelle et al. 2012).

5.4.2 *Organic Farming and Conventional Farming*

Organic farming management could be considered as the oldest way of agricultural management. However, a resurgence in interest in organic farming occurred at the beginning of the twentieth century (around 1920) in the USA. The term of “organic farming” appeared around 1950 and this production management has been really organized at worldwide scale since 1972 due to the creation of the International Federation of Organic Agriculture Movements (IFOAM). The creation of this federation gave a real professional and institutional recognition of organic farming (OF). Moreover, since 1999, it has been included in the *Codex alimentarius* (Griffon 2013). The marketing of organic products is regulated by quality-labels based on norms from IFOAM. These labels do not really deal on the quality of the product, but focus on the respect of environment.

The objective of organic farming is to develop a sustainable agriculture, in terms of economy and environmental impact, and to propose a self-sufficient system in terms of energy and biology instead of reliance on exogenous inputs of fertilizers (Watson et al. 2002). From a technical point of view, this management (i) forbids the use of synthesis products (e.g. fertilizers, pesticides), (ii) uses long crop rotation and more diverse crop rotation, (iii) recycles the farm effluents (farm manure and/or slurry) and crop residues, (iv) applies green amendments (Shepherd et al. 2002). Moreover, organic farming relies on biological or mechanical pest and weed control (i.e. by plowing) and natural nitrogen fixation (Shepherd et al. 2002).

More than 37 million ha of farmland are under organic management worldwide. However, the importance is extremely variable within continent: 12.1 million ha in Oceania, 10.3 million ha in Europe, 8.4 million ha in South America, 2.8 million ha in Asia, 2.7 million ha in North America and 1.1 million ha in Africa. Moreover, there is an extreme variability within each continent. In Europe, the percentage of surfaces managed under organic farming range from 1.8 % in Romania up to 20 % in Denmark (AgenceBIO 2009).

5.4.2.1 *Impact of Organic Farming on Soil Biodiversity*

The analysis of the impact of organic farming is not easy because under organic farming there are many different types of production (e.g. crop, vineyards, orchards, mixed-farming and breeding, truck farming). Each of these types of production has

its own constraints and practices which can also act on biodiversity. The published meta-analysis dealing with several biological groups such as birds, plant, insects and soil organisms (Bengtsson et al. 2005) revealed the huge complexity of data analysis of organic farming compared to conventional farming. Concerning the diversity, this study showed that organic farming usually increases species richness, having on average 30 % higher, but the results were variable among studies, and 16 % of them showed a negative effect of organic farming on species richness. It appeared that on average, organisms were 50 % more abundant in organic farming systems, but the results were highly variable between studies and organism groups. Birds, predatory insects, soil organisms and plants responded positively to organic farming, while non-predatory insects and pests did not. Therefore, this synthesis revealed that organic farming has often, but not always, positive on species richness and abundance, but that its effects are likely to differ between organism group and landscape, and also investigation-scale. The authors suggested that positive effects of organic farming on species richness can be expected in intensively managed agricultural landscapes, but not in small-scale landscapes comprising many other biotopes as well as many agricultural fields.

Therefore, in the following examples, we will try to give a wide range of results by focusing on some specific agricultural systems.

5.4.2.2 Organic Vineyards

The rate of conversion of conventional vineyards into organic farming is increasing. In France, from 2001 to 2008, the area of organically managed vineyards increased by 110 % (AgenceBIO 2009). This results in modification of agricultural practices such as the application of organic manure, the use of tillage or grass-cutting to control weeds and the application of natural pesticides with preventive action (Coll et al. 2011). In order to reduce the pressure of mildew, which is the most prevalent diseases encountered in vineyards, organic winegrowers use fungicides based on naturally occurring materials (e.g. sulphur dust, micronized sulphur), canopy management, predictive models for the disease are based on temperature, and monitoring of the disease in the vineyards as components of their powdery mildew control program (McGourty 2008). However, there is a tolerance for the use of “Sulfate of copper” (copper fungicide) but at very limited doses.

Although the increase of vineyards conversion into organic farming, scientific knowledge concerning the effect of organic viticulture on soil biodiversity is still scarce, except the study of Probst et al. (2008), Reinecke et al. (2008) and Coll et al. (2011). However requests from winegrowers for a better understanding of the impact of their practices on soil functioning, are increasing. In order to address these requests, since the beginning of 1980, many research programs have been conducted in the famous region of Champagne (France), supervised by CIVC (Interprofessional Committee of Champagne Wines). One of these research programs compared an organic vineyard production (biodynamics), an integrated vineyard production (less pesticide application and organic fertilization) and a conventional vineyard production. After 6 years, this work revealed that integrated system and

organic system were beneficial to microbial biomass. They also positively altered the earthworm community more than conventional system, however the integrated system was much more favorable with the highest abundance (respectively 100.2 individual m^{-2} , 38 individual m^{-2} , and 16.6 individual m^{-2}), highest biomass (respectively 47.3 g m^{-2} , 11.1 g m^{-2} , and 4.3 g m^{-2}); both organic and integrated systems increased the number of species and the evenness (Georget et al. 2006). These results were explained by (i) the negative impact of deep plowing under conventional and organic vineyards (Evans and Guild 1948; Pérès et al. 2010), (ii) the high application of copper sulfate (Bordeaux mixture) which led to soil contamination by copper (Ablain 2003) and application of pesticides under conventional system (Cluzeau et al. 1987; Cluzeau and Fayolle 1988), (iii) the organic fertilizer application under integrated vineyard (Pérès et al. 1998). These results were confirmed by other results observed under “Beaujolais” vineyards after 4 years of system differentiation (Pérès and Cluzeau 2009). A research study conducted in another French region (the Languedoc-Roussillon region), demonstrated that organic farming led to an increase in soil microbial biomass, plant-feeding and fungal-feeding nematodes density, while decreased endogeic earthworm density due to the increase of soil compaction (Coll et al. 2011). The positive impact of organic farming on microbial biomass was also supported by studies carried in East part of France (the region of Colmar), while the microbial activity (respiration) was adversely affected (Probst et al. 2008). In South Africa, organic farming appeared to promote soil fauna activity (feeding) by the preservation of more favourable moisture conditions (Reinecke et al. 2008). All of these results demonstrate that within organic farming systems there are very different vineyard practices which can positively or negatively impact soil biodiversity.

5.4.2.3 Organic Crop System

Results from thirteen Dutch organic farms shows that organic management resulted in significantly higher numbers of bacteria of different functional groups as well as larger species richness in both bacteria and nematode communities and more resilience to a drying–rewetting disturbance in the soil (van Diepeningen et al. 2006). This study supported other previous results which revealed that organically managed soils had a higher diversity of bacteria (Drinkwater et al. 1995; Mäder et al. 2002), arbuscular mycorrhizal fungi (AMF) in agrosystems (Oehl et al. 2003), nematodes (Mulder et al. 2003), earthworms (Mäder et al. 2002) and insects and arthropods (Asteraki et al. 2004; Drinkwater et al. 1995; Mäder et al. 2002) than conventionally managed soils. Moreover, a higher microbial activity (Mäder et al. 2002; Workneh et al. 1993) and microbial biomass (Mäder et al. 2002; Mulder et al. 2003) were found in organic soils. However, contrasted results were also observed. Some authors found no differences in bacterial biodiversity (Lawlor et al. 2000) or in fungal communities (Franke-Snyder et al. 2001) between organically or conventionally managed soils. A study realized in Germany under six different crops rotations (Schrader et al. 2006) showed that, after 3 years of conversion

towards organic farming, microbial biomass and collembolan abundances were lower in organically farmed fields, although the collembolan diversity was generally higher (22 species vs. 20 species) combined with a shifting in the dominance structure of the species which leads to higher evenness (0.79 vs. 0.70). These authors underlined that the impact of organic management is a long term processes: after 3 years of management conversion, the soil biota was still changing. All of these results confirm the huge complexity and diversity of biological responses under organic farming systems (Bengtsson et al. 2005).

5.4.2.4 Organic Grassland Farming

A recent study was conducted in three different regions in Germany in order to assess the impact organic grassland farming on plant diversity and arthropod diversity (Klaus et al. 2013). The results showed that arthropod diversity was significantly higher under organic than conventional management. On the contrary, arthropod abundance and vascular plant diversity did not considerably differ between organic and conventional grasslands. Moreover, yield and fodder quality did not considerably differ between organic and conventional grasslands, which is in contrast to some critics of organic management who argue that restricted fertilizer input may significantly reduce quantity and quality of yields (Offermann and Nieberg 2000). Moreover, this study showed that permanent grasslands responded slower and probably weaker to organic management than crop fields did.

5.4.3 From Forest Ecosystem to Agroforestry Systems

Agroforestry or pastoral-sylviculture is an integrated approach of using the interactive benefits of combining trees and shrubs with agriculture (crops or livestock farming). It combines agriculture and forestry technologies to create more diverse, productive, profitable, healthy, and sustainable land-use systems. Agroforestry systems can offer increased productivity, economic benefits, and more diversity in the ecological goods and services provided (Dupraz and Liagre 2008).

Agroforestry represents a wide diversity in application and in practice (Wojtkowski 1998). Although agroforestry system includes trees in its design, the agrosystem is very different compared to forest ecosystem, in terms of functioning and management. The sustainability of agroforestry systems depends on the knowledge of both forest and agriculture.

5.4.3.1 Forest Ecosystem

Terrestrial ecosystems classified as forest represent some 40 million km² and 30 % of the global land use. Combining woodland and pasture, these ecosystems represent more than half of the global land use, while agricultural crops represented 11 %

(Whalen and Sampedro 2010). Forest plantations have exceeded 264 million hectares and are under intensive management (FAO 2010). Although less intensively managed than agrosystems, these ecosystems are modified by natural and anthropogenic processes. These processes impact both the global functioning of the systems and also their biodiversity. Forest soils under temperate climates are different from cultivated soils or pastures according to three points of view: (i) fertile soils have been commonly used for cultivation of crop while forests are developed on poor soils, more often with extreme pH (acid or very basic), (ii) under agrosystems, the use of fertilizers and the mechanical actions strongly impact the ecosystem, while under forest the impact is limited, (iii) forests present permanent plants, the trees, which depending on tree species, influence soil on long term. All these parameters lead to specific habitat for soil biodiversity.

5.4.3.2 How Can Soil Biodiversity and Functions Be Impacted in Forest Ecosystem?

In forest ecosystem, the density and community structure of soil organism are strongly impacted by the tree species, the management (plantation and wood exportation which lead to soil compaction), natural constraints (fire) and the physico-chemical characteristic of soil (Uroz et al. [submitted](#)).

The tree species have a strong impact of soil biodiversity and therefore on soil functioning. In Brazil, the study conducted by da Cunha Neto et al. (2012) which compared soils invertebrates under five vegetation types demonstrated the strong influence of land use and vegetation species on organism community structure, and revealed the positive impact of mimosa on soil fauna density. In a French study (Arpin and Ponge 1986), the comparison between a plantation of sessile oak (*Quercus petraea*), a mature *Pinus sylvestris* plantation and a mixed plantation of *Q. petraea* and *P. sylvestris*, clearly showed the impact of the tree species composition on soil invertebrates community composition (density and proportion of the different functional groups), their vertical distribution and therefore their activity, leading to the development of different forms of humus. *Pinus sylvestris* presented a dysmoder humus, oak plantation presented a acid mull humus, and mixed plantation presented a mull-moder humus. This study concluded that mixed plantations reduced accumulation of organic matter on the soil surface. Moreover, another study carried in the same sites shows that the relationship between soil fauna and soil characteristics is very complex and appears to be strongly dependent of the biological group: meso- and microfaunal populations (e.g. Collembola, mites and nematodes respectively), which are mostly dependent on the transformation of humus type under pine-trees, while macrofaunal populations (earthworms, isopoda, insects) are rather dependent on the higher quality forest litter of mixed tree species (Arpin et al. 1986).

Fertilisation is also very important. One of the main types of mineral fertilisation corresponds to liming in order to increase the pH. In fact, calcium input promotes earthworms (increase of density, especially for anecic species), however it is essentially benefit to the indigenous community, but it does not stimulate colonisation

by new species which can modify the evolution of the humus form, except if these species are located in the vicinity of the area or are inoculated into the area (Ponge 2009).

Impact of Harvesting

Harvesting forest combines the remove of organic matter (trunks, branches, small wood) and the soil compaction due to the use of heavy machines. The removal of the organic matter results in the decrease of the nutrient provision due to the interruption of their recycling; it also results in a simpler habitat which immediately reduces food supply and diversity, shelter and reproduction sites for fauna (Guerrat et al. 1982; Souto et al. 2008; da Cunha Neto et al. 2012). Moreover, the protection of the vegetation against microclimate variation is reduced, which results in high insolation, extreme soil temperatures and low moisture, making the environment less favourable for survival and reproduction (Guerrat et al. 1982). The regeneration of forests after cutting activities is strongly influenced by the intensity of harvest and secondary practices such as burning, herbicide application, and replanting the area with selected tree species (e.g. fast growing pines, spruce and hybrid poplar). Moore et al. (2002) demonstrated that there are few negative impacts associated with low intensity selective cutting and strip clearcutting on the abundance of soil fauna in a northern hardwood forest stands 6–12 years after harvest.

Soil compaction, due to the use of heavy machines, strongly disturbs soil structure by decreasing the macroporosity and therefore modifies air and water movement, and also soil habitat quality. This environmental perturbation, impacts on soil micro-organism community structure and therefore on the biological soil functioning. In a study conducted in beech and spruce forests, soil compaction led to an increase of methane production due to the increase of methanogenic bacteria; the size of the bacteria community was stable 1 year after compaction suggesting the persistence of the processes (Frey et al. 2011). Indeed, soil compaction creates habitats which are more suitable for organisms adapted to anoxic conditions or supporting low concentration of oxygen, such as methanogenic bacteria or sulfate-reducing bacteria, while it reduced the development of fungi.

The removal of organic matter combined with the compaction of soil could lead to a huge decrease of carbon (from 51 to 84 % compared to the control) and an increase of bulk soil density (from 4 to 20 %) (Hartmann et al. 2012). These environmental perturbations strongly modify the microorganism community and the removal of organic matter is the stronger driver.

Impact of Fire

Globally, more than 350 millions of hectares of vegetation are subjected to fire every year, and more than a half in Africa. Concerning tropical forests (1.8 billion hectares), from 150 to 250 millions are destroyed every year due to savage fires.

In Mediterranean regions, from 700,000 to 1 million hectares of vegetation burn every year (FAO 2009). Fire impacts forest ecosystems by the destruction of the vegetation, the death of animals and modification of soil characteristics. In fact, the first effect is that fire quickly produces more available nutrients and organic matter, which therefore improves soil fertility. However, this beneficial impact is very short lived. Furthermore, the impact of fire is strongly related to the frequency of fires: in a French forest (dominated by oak) associated with maquis, fires separated by more than 100 years allow the rebuilding of organic matter stock (more than 5 cm thickness); between 100 years and 25 years, soil fertility, organic matter stock and biological activity are low but constant; when the frequency is more than one fire every 25 years, biological communities are very poor, chemical and physical properties are strongly altered and tree cover partially disappeared and resilience is reduced (Vennetier et al. 2008).

5.4.3.3 Agroforestry Systems

Although agroforestry systems could be considered as older agrosystems (Dupraz and Liagre 2008), until now scientific knowledge concerning their effects on soil functioning and especially soil biodiversity is scarce and very recent.

The positive effects of agroforestry system have been underlined in Honduras (Pauli et al. 2011). This study reported that smallholder agroforestry systems (for maize, beans and sorghum) can retain relatively abundant, diverse populations of soil invertebrates. For the study, soil macrofauna were sampled across agroforestry fields that had been converted from secondary forest from between 2 to 10 years previously. The results showed that abundance and diversity of soil fauna remained relatively constant across fields of different ages, and that the biomass of soil macrofauna increased in agroforestry fields that had recently been converted from forest. These positive results could be explained by the land management practices, such as continuous soil cover, the presence of diverse trees and other vegetation within cropping fields, the use of mulch, and the presence of a mosaic of habitat types in the surrounding area.

In Brazil, a recent study (Coimbra Manhaes et al. 2013) showed that the development of a litter layer by leguminous tree plantations on degraded pasture resulted in a higher abundance and diversity of soil fauna such as social insects (Formicidae) and microbial grazers (Collembola). In China, Zhao et al. (2013) showed that the addition of *Cassia alata* (a legume shrub) improved soil food web structure by increased the abundance of the high trophic-level through nematodes (omnivorous) and mites (predator); this improvement was also related to an increase of nitrogen in the soil, due to the nitrogen fixation by legumes. In contrast, removal of forest understory plants caused a serious disturbance of the ecosystem by increasing soil temperature, reducing soil moisture, decreasing soil respiration and suppressing high-trophic groups of soil invertebrates (destruction of predatory and omnivorous nematodes) (Li et al. 2010; Wang et al. 2011; Wu et al. 2011; Zhao et al. 2011).

All of these results are encouraging for the future and the development of agroforestry systems. However, due to the high variability of agroforestry systems, more data are necessary to have an overview of the variability of the biological response and to produce a tool for stakeholders.

5.5 Conclusion

The maintenance or the restoration of soil biodiversity is one of the challenges for the future, as soil biota are essential for many soil processes and functions. However, as described in this chapter, the task is difficult because the impact of soil managements (industrial, agricultural) on soil organisms differ considerably depending on (i) biological aspects such as the body size of the organisms, the adaptation to certain soil properties, the habitats demands and food preference, and (ii) the nature and intensity of the perturbations (e.g. type of pollution, intensity and frequency of ploughing, harvesting). Moreover, there is a strong spatial and temporal heterogeneity of biota responses linked for part to the high variability of soils (pH, texture, organic matter content). Sustainable agriculture seeks to produce optimal yields with good economic returns and at the same time maintain soil quality; the challenge will be how to sustain this biological equilibrium (Andrade et al. 2003). This chapter describes the impact of agricultural practices on soil biodiversity and highlights some promising managements. However, more data are needed and the development of monitoring approaches, based on soil indicators such as bioindicators, have to be encouraged in order to support policy and decision making towards the sustainable management of soils across the world (Pérès et al. 2008; Bispo et al. 2009; Pérès et al. 2011; Rutgers et al. 2009). The next step will be to interpret biological soil indicators in terms of ecosystem services (Rutgers et al. 2012). One promising avenue is based on ecological traits i.e. morphological, physiological, behavioural or life-history attributes to organisms. This approach will allow a better mechanistic understanding of the relationships and possible generalization across eco-region, independent of taxonomy (Pérès et al. 2011; Brussaard 2012; Pulleman et al. 2012).

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Chapter 6

Root Pathogens

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Abstract Root pathogens affecting root systems of living plants are represented by a taxonomically wide array of organisms, including viruses, protozoa, chromists, fungi, nematodes, and plants. A number of root pathogens function also as vectors of viruses. In addition to the well-known, widely spread species from agriculture, probably many are still hidden in unmanaged vegetations given their limited ability for dispersal and problems associated with identifying functions of pathogens in plant species mixtures. Key ecological traits of root pathogens include host range, mode of dispersal and survival, saprotrophic ability, and temperature and moisture requirements for growth and survival. Several evolutionary convergent traits occur for root pathogens, because they share general properties of soil life, including the relative difficulty to move within the soil and, from this, the need to survive for prolonged periods of time under adverse conditions. Saprotrophic activity by the pathogen may occur, often on dead organic material originating from its own host. There are various survival structures (single- and multicelled) that combine a very low maintenance respiration with inaccessibility for infection by other organisms. Also soil biostasis, the phenomenon of non-germination of viable propagules in a living soil, contributes to the longevity of soil-borne pathogens. Generally dispersal in soil is in the order of magnitude of meters per year; long-range transport is primary caused by transport of infected plant material or infested soil. Some root pathogens fruit aboveground and then spores will become airborne, and thus transported over considerably larger distances.

Infection incidence and severity by root pathogens depends on the abiotic environmental conditions (mainly temperature, soil moisture content and pH), inoculum density, amount of susceptible host tissue and activity of antagonists. Under optimal conditions, root pathogen populations accumulate, creating an environment that is unfavourable for susceptible successors. This general phenomenon forces farmers

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to introduce crop rotations, and causes young plants to grow less well near mature trees, or at places where mature trees have been removed. On the other hand, lack of root pathogens explains the success of bioinvasive plants in a number of cases. In unmanaged, natural vegetations, root pathogens may survive in perennial root systems. Their effects are much less clear than in agriculture, since they can be replaced by resistant or less susceptible plant species before they die. The role of root pathogens in unmanaged vegetations has been addressed only marginally, but their role is potentially large. A clear indication that pathogens play a role in unmanaged vegetations is that overyielding of root biomass in species mixtures as compared to the sum of root biomass production in monocultures of the respective species has been observed repeatedly. Overyielding could be removed by application of fungicides to the soil. Where pathogens limit the development of certain plant species, they leave space for other plant species, thus promoting vegetation diversity in space or in time. Ecological concepts on root pathogens have been developed mainly on the basis of agronomic problems but these may differ for unmanaged vegetation. Especially the uncultivable pathogens require more attention.

6.1 Introduction

Root pathogens are organisms affecting root systems of plants. Wherever hosts of root pathogens occur in large densities they are more likely to become attacked. Root pathogens inflict enormous economic losses in agricultural production (Oerke 2006), which explains why they have received much attention in agroecosystem research. Currently their functions in natural ecosystems are also becoming appreciated (Gilbert 2002; de Kroon et al. 2012). Root pathogens are not the single cause of reduced root performance. Other soil-related factors reducing crop growth include suboptimal soil conditions (e.g. low level of available nutrients, poor soil structure), absence of essential mutualists (e.g. symbiotic N-binding bacteria in leguminous plants) and plant-mediated allelopathic effects. Naturally also aboveground conditions affect root growth, like reduced light conditions and airborne pest and pathogen organisms.

Often root pathogens are referred to as soilborne pathogens, but the latter refers to their habitat of survival (the soil) as opposed to airborne pathogens. The difference is rather subtle, but there are soilborne pathogens that, upon germination of soilborne survival structures, sporulate aboveground followed by shoot infection (e.g. *Sclerotinia sclerotiorum*) or which, after root infection, colonize the shoots where they sporulate (e.g. *Fusarium oxysporum* f. sp. *basilici*; Gamliel et al. 1996). Likewise, some airborne pathogens are able to infect belowground plant tissue, such as *Phytophthora infestans* infecting belowground potato tubers.

The term plant pathogen refers to biotic or abiotic factors causing plant disease. A diseased plant is a plant that is not performing well. The pathogenic nature of many plant parasites can be seen easily in many agricultural systems. For example,



Fig. 6.1 Focus of *Meloidogyne hapla* in a carrot field

many plant pathogenic nematodes can incite total crop failure (Fig. 6.1). On the other hand, in natural systems the role of root pathogens is almost always obscure, because diseased plants are likely to be outcompeted by non-diseased plant species prior to their death. Thus the interpretation of root pathogens is different: in agricultural systems they are the main reason for crop rotation (i.e. the alternation in time of crop species that vary in susceptibility to a given pathogen) (Bennett et al. 2012), while in natural systems they are valued as potential drivers of vegetation diversity (Chesson 2000).

The pathogenic nature of an organism is usually established by infection experiments. An organism is regarded pathogenic if it follows Koch's Postulates (Agrios 2005):

- the plant performs less well in its presence;
- the pathogen can be isolated from the symptomatic material;
- the isolated pathogen incites the same disease symptoms if it is inoculated into a healthy plant;
- the pathogen can be isolated from this inoculated, diseased plant.

Although Koch's Postulates look on first sight straightforward, proving the pathogenic nature can be difficult when pathogens are non-cultivable, when multiple causes are acting simultaneously, or when infection only occurs under unfavourable plant growing conditions (e.g. shortage of nutrients).

There is a plethora of organisms affecting root systems negatively. Here, we exclude mammal predators like rodents and moles. For the sake of simplicity we classify all nematodes that derive nutrients from plants as pathogens, although for a range of species it would be more correct to refer to them as herbivores.

6.2 Examples of Root Pathogens

Major root pathogens occur in a remarkably wide range of taxa, including the prokaryotes (bacteria), the protozoa (kingdom Protoctista, division Plasmodiophoromycota, plasmodiophoromycetes), chromists (kingdom Chromista, division Oomycota, oomycetes, previously classified as fungi, also referred to as fungal-like organisms), fungi (kingdom Fungi; divisions Chytridiomycota (chytridiomycetes), Ascomycota (ascomycetes) and Basidiomycota (basidiomycetes)), plant parasites (kingdom Plantae) and nematodes (kingdom Animalia, phylum Nematoda), as well as several virus species (Table 6.1). A relatively small number of pathogens can infect root systems only with a vector (Table 6.1). For some groups, intraspecific classification (i.e. classification below the species rank) is crucial: examples include the fungal species *Fusarium oxysporum* and *Thanatephorus cucumeris* (= *Rhizoctonia solani*). The great majority of spores of *F. oxysporum* encountered in soil are not plant pathogenic and only a minority are able to infect root tissue. Since morphological differences between pathogenic and non-pathogenic strains are absent, and since pathogenicity even towards a single host can be polyphyletic (Mes et al. 1999), the species concept is still maintained at the morphological level. The same is true for *T. cucumeris*, which is differentiated into anastomosis groups (AGs) on the basis of vegetative incompatibility of agar-cultivated mycelia. The situation is complicated as it appeared functional to differentiate AGs into sub- and subsub-groups which, respectively, show poor vegetative incompatibility (Schneider et al. 1997). These subdivisions have appeared functional as these exhibit highly different ecological traits in e.g. host range and temperature characteristics.

In addition to the soil-borne pathogens well-known from agriculture, probably many more pathogens are still hidden in unmanaged vegetations. Without doubt in nature a wide range of pathogens occur which are different from those commonly found in agriculture. In addition many species may occur only locally, given their limited ability for spatial dispersal. The ecology of pathogens in unmanaged vegetations is challenging as the development of bioassays can be time-consuming, especially if the pathogen cannot be cultivated *in vitro* (e.g. the Plasmodiophorales, with many species occurring in nature; Karling 1968) or if the host is difficult to grow.

6.3 Function of Root Pathogens

Root pathogens can be characterized by their host range, mode of dispersal and survival, saprotrophic ability, and temperature and moisture requirements for growth and survival. There are several evolutionary convergent traits of taxonomically unrelated root pathogens, because they share general properties of soil life, including the relative difficulty to move within the soil and, from this, the need to survive for prolonged periods of time under adverse conditions (e.g. absence of an appropriate host or occurrence of drought or frost) (Termorshuizen and Jeger 2008).

Table 6.1 Examples of root pathogens

Species	Disease	Host range	Distribution	Virus transmission
Kingdom Protoctista, division Plasmodiophoromycota				
<i>Spongospora subterranea</i> f. sp. <i>subterranea</i>	Powdery scab	Potato	Worldwide, mainly in cool and moist regions	Potato Mop-Top Virus, causing potato mop-top
<i>Polymyxa betae</i>	Rhizomania	Sugar beet	Worldwide	Beet Necrotic Yellow Vein Virus, causing rhizomania
<i>Plasmodiophora brassicae</i>	Clubroot	Cruciferae (e.g. cabbage)	Worldwide on neutral to acidic soils	None
Kingdom Chromista, division Oomycota				
<i>Aphanomyces euteiches</i>	Root rot	Legumes	Worldwide	None
<i>Phytophthora cinnamomi</i>	Root rot	Many	Worldwide	None
<i>Phytophthora nicotianae</i>	Seedling damping-off	Many	Worldwide	None
<i>Pythium</i> species	Root rot and seedling damping-off	Many	Worldwide	None
Kingdom Fungi				
<i>Synchytrium endobioticum</i> (Chytridiomycota)	Potato wart	Solanaceae (e.g. potato)	Worldwide, mainly Europe	None
<i>Olpidium brassicae</i> (Chytridiomycota)	None, only vectoring viruses	Many, e.g. lettuce	Worldwide	Several, e.g. Lettuce Big Vein Virus, causing big vein
<i>Cylindrocarpum destructans</i> (Ascomycota)	Root rot	Many	Worldwide	None
<i>Fusarium oxysporum</i> , <i>F. redolens</i> , <i>F. solani</i> (Ascomycota)	Fusarium wilt or Fusarium root rot	Many	Worldwide	None
<i>Macrophomina phaseolina</i> (Ascomycota)	Black dot or charcoal rot	Many	(Sub)tropics	None
<i>Verticillium dahliae</i> (Ascomycota)	Verticillium wilt	Most dicotyledonous plants	Worldwide except in tropical climates	None

(continued)

Table 6.1 (continued)

Species	Disease	Host range	Distribution	Virus transmission
<i>Thanatephorus cucumeris</i> (= <i>Rhizoctonia solani</i> ; Basidiomycota)	Root rot, damping-off	Many	Worldwide	None
<i>Armillaria mellea</i> sensu lato (Basidiomycota)	Tree root rot	Many woody species	Worldwide	None
Kingdom Plantae				
<i>Orobanche cumana</i>	Broomrape	<i>Helianthus</i>	Eurasia	None
<i>Striga</i> spp.	Purple witchweed	Grasses	Africa	None
Kingdom Animaliae, phylum Nematoda				
<i>Meloidogyne</i> species	Root knot	Many	Worldwide	None
<i>Globodera pallida</i> , <i>G. rostochiensis</i>	Potato cyst nematode	Solanaceae, incl. potato	Worldwide	None
	Root lesion nematode	Many	Worldwide	None
<i>Trichodorus</i> and <i>Paratrichodorus</i>	Stubby root nematodes	Many	Tobraviruses, e.g. Tobacco Rattle Virus	Worldwide
Viruses				
Tobacco Mosaic Virus	TMV	Many	Worldwide	–

The host range is very different among root pathogens. Pathogens like *Macrophomina subterranea* (black dot), *Meloidogyne hapla* (root knot nematode), *Verticillium dahliae* (wilt), some anastomosis groups of *Thanatephorus cucumeris* (root rot or damping-off) and *Striga* (obligate plant parasite) have wide to very wide host ranges including hundreds to thousands of hosts. On the other hand, there is also an array of economically important pathogens possessing a remarkably narrow host range, e.g. *Spongospora subterranea*, of which the forma specialis *subterranea* only infects potatoes, *Orobanche cumana* (broomrape) infecting only sunflower (*Helianthus*), and *Polymyxa betae* only infecting *Beta* species including sugar beet. Most pathogens with a narrow host range are obligate parasites (i.e. they have no saprotrophic ability whatsoever and can consequently not be cultivated *in vitro*, e.g. *Orobanche cumana*, *Polymyxa betae*, *Synchytrium endobioticum*) and have highly persistent survival structures. On the other hand, pathogens with a wide host range are ecologically obligate (i.e. depending for growth on a living host, but cultivable *in vitro*, e.g. *Macrophomina subterranea*, *Verticillium dahliae*) or facultative parasites (i.e. to some extent living on dead organic matter and cultivable *in vitro*, e.g. *Phytophthora* spp., *Pythium* spp., *Thanatephorus cucumeris*) with a varying level of persistence of survival structures. These generalizations are probably biased towards arable systems, where host roots are not present throughout the year.

Saprotrophic activity by the pathogen may occur, and can be crucial for survival in the absence of a host. Saprotrophic activity is only possible if the pathogen is able to compete with pure saprotrophs for dead organic matter, hence the term competitive saprotrophic survival (Garrett 1951, 1970). Typically, saprotrophic activity is limited to growing on dead organic matter of its own host. For this behaviour the now rarely used term perthotrophy has been coined. On other substrates saprotrophic activity is usually limited because of the presence of a large population of soil microorganisms able to colonize that substrate. Thus perthotrophy is probably the main means by which some root pathogens can exhibit activity outside the living host tissue. An example of a perthotrophy is *Armillaria mellea*, the shoestring fungus, which typically continues to grow for several years on the woody substrate it has killed (reviewed by Termorshuizen 2000). The nutrients thus obtained are used for short-distance exploration of the soil by long-lived, shoestring-like survival structures, the rhizomorphs, as well as for long-distance exploration by the massive formation of basidiospores in aboveground appearing fruiting bodies. Pure saprotrophy by pathogens is hampered by the presence of massive numbers of carbon-starved microbial populations specialized in saprotrophism, which can be illustrated in simple experiments by comparing the pathogen's activity in sterilized soils with that in unsterilized soils. Still, saprotrophic growth of root pathogens can be important especially if there is a large supply of organic matter from fresh crop residues or when environmental conditions are selectively beneficial to certain pathogens. Large supplies of fresh organic matter occur mainly in agriculture, e.g. where green manure crops are sometimes incorporated into the soil. This may stimulate pathogens like *Pythium* and *Thanatephorus cucumeris*, and can lead to attack of subsequently appearing

seedlings of the next crop (Manici et al. 2004; Bonanomi et al. 2007). Environmental conditions like high soil moisture content can further select for pathogens that can tolerate low oxygen pressure, like *Pythium* and *Phytophthora* species (Martin and Loper 1999). Under such conditions, their dispersal is also favoured because of their ability to form zoospores, one-celled flagellate spores, which can actively move through water.

Resting structures combine a very low maintenance respiration (Mondal et al. 1996; Mondal and Hyakumachi 1998) with inaccessibility for other organisms caused by the cell wall structure (Cooke and Whipps 1993). Examples include one-celled structures (e.g. resting spores formed by *Plasmiodiophora brassicae* and *Synchytrium endobioticum*), simple few-celled (e.g. chlamydospores formed by *Fusarium oxysporum*) or multi-celled structures (e.g. sclerotia formed by *Macrophomina phaseolina* and *Sclerotium rolfsii*, microsclerotia by *Verticillium dahliae*), more complex multi-celled structures with specialized cells (e.g. *Sclerotinia sclerotiorum*), cysts by cyst nematodes (e.g. *Globodera* and *Heterodera* spp.), and egg masses by root knot nematodes (*Meloidogyne* spp.). Parasitized plants often form seeds that can survive for a prolonged time in soil. The tree-infecting *Armillaria mellea* forms unique, persistent, melanised, shoestring-like rhizomorphs that form extensive networks within soil (Lamour et al. 2007). The way resting structures are reactivated varies (reviewed by Rasmann et al. 2012): either activation is based on a signal from the rhizosphere (probably a relatively high concentration of simple carbon compounds, including CO₂) or, associated with these gradients, a pH gradient (cf. Wang et al. 2009), or by a specific signal. In the case of a specific signal, the resting structures are easy to germinate *in vitro*. Usually this tactic applies for wide host range pathogens, for which it does not matter which plant species is producing the stimulus. For some tropical root-knot nematodes (*Meloidogyne* spp.) with extraordinary wide host ranges, the only (or main) stimulant seems to be temperature (Perry and Wesemael 2008), as this generally correlates with germination and growth of plants.

In all unsterilized soils, even survival structures that germinate readily *in vitro* are restricted in their activity. This was originally referred to as soil fungistasis, but as it applies also to other soil organisms, the term general soil biostasis is more appropriate. It is effective in keeping survival structures inactive in the absence of activation compounds and is most likely caused by withdrawal of nutrients (through microbial activities) and production of biostatic (or fungistatic) compounds (Garbeva et al. 2010). In the rhizosphere, soil biostasis is relatively low, probably because of the presence of easily accessible root exudates. The interplay between rhizosphere effects (amount and type of root exudates and composition of rhizosphere inhabitants) and soil biostasis effects (actual and potential activity of soil micro-organisms) determines the rhizosphere volume within which pathogens germinate (referred to as the pathozone according to Gilligan and Bailey 1997). Exploitation of general soil biostasis to manage root pathogens has been applied with variable rates of success. The general thought was that, once resting structures could be stimulated to germinate in the absence of a host, e.g. with organic amendments, they would die off. This phenomenon is referred to as lysis-after-germination, as was

found for chlamydospores *Fusarium oxysporum* f. sp. *elaeidis* after addition of various organic amendments (Oritsejafor and Adeniji 1990). However, the opposite can occur as well, i.e., upon germination, the pathogen grows and subsequently forms new resting structures, as was shown for *F. oxysporum* f. sp. *cubense* (causing banana wilt) after application of chicken manure (Nasir et al. 2003), ending up with increased levels of pathogen inoculum. On the other hand, non-host plants that induce germination of root pathogens are being applied widely. Examples include hatching of *Globodera* sp. (Potato Cyst Nematode) by resistant potato cultivars or by early harvest of susceptible cultivars (prior to development of the next generation of the nematode) or germination of microsclerotia of *Verticillium dahliae* in the rhizosphere of non-host cereals. Another mechanism of pathogen-reducing crops is the reduction of populations of *Pratylenchus* by growing *Tagetes* (marigold), which is based on intoxication of the nematodes upon penetration of the roots (Evenhuis et al. 2004).

For narrow host range pathogens it is more common that resting structures do not depend on general soil biostasis but that they instead are activated by a host-specific signal. Examples include sclerotia from *Sclerotium cepivorum*, the causal agent of onion white rot, which remain dormant until germination is triggered by diallyl-disulphide present in the root exudates of *Allium* roots (Entwistle et al. 1982) and *Globodera* spp. (Potato Cyst Nematode), which remain dormant until germination is triggered by so-called Hatching Factors (Turner and Rowe 2006; Rasmann et al. 2012). Compounds that hatch soilborne nematodes may be present in the water and the gas phase, which may be active at different spatial scales (Rasmann et al. 2012).

From all this, the general picture of the life cycle of root pathogens appears, of which the major driving force is their dynamics in soil. Either pathogens are using soil just as a place to survive until a host root develops nearby ('root pathogens' *sensu* Garrett (1951, 1970)) or the pathogen can survive with some saprotrophic activity in soil, usually as perthotrophs ('soil pathogens' *sensu* Garrett (1951, 1970)). Furthermore pathogens may spread passively (zoospores of chromists, protozoa and chromists) or actively (nematodes) in water, or spread by root to root contact (e.g. *Gaeumannomyces graminis* (Gosme and Lucas 2009), *Fusarium oxysporum* f. sp. *radicis-lycopersici* (Rekah et al. 1999) and *Pythium violae* (Suffert and Montfort 2007)). The typical distance bridged is small (meters per year). Natural long-range transport may occur by dust storms or infested seeds. Without doubt the main responsible factor for long-range transport, including intercontinental dispersal, is transport of infected plants and infested soil. Root pathogens multiply only in massive numbers after having acquired food from host plants. Root-infecting fungi causing wilt (e.g. *Fusarium oxysporum* and *Verticillium dahliae*) typically produce their survival structures in shoot tissue, which return to soil after death of the plant. These survival structures are often formed in large numbers. For example, in 1 g of air-dry potato stem tissue, approx. 1 million microsclerotia of *Verticillium dahliae* occur (pers. obs. A.J. Termorshuizen, unpublished). Based on an estimated amount of 2,200 kg ha⁻¹ of dry weight of potato stem tissue at harvest (= 50 g per plant), there would be 2.2×10^{12} microsclerotia ha⁻¹. If these would all survive, one would expect 1,100 microsclerotia cm⁻³ of soil in the top 20 cm soil layer, while typical

numbers for severe soil infestations are in the order of 10–100 microsclerotia cm^{-3} of soil, indicating that a great portion of microsclerotia is inactivated quickly. Little, if any, work has been performed on this phenomenon.

6.4 Ecology of Root Pathogens

Root pathogens infect plants only within a certain range of temperature and soil moisture. Their effects on number of infected plants (disease incidence) or on severity of disease depend on their density (inoculum density) which in turn is affected by the activity of antagonists (e.g. Oyarzun et al. 1997; reviewed by Jeger and Termorshuizen 2012). Pathogens do not necessarily cause death of the host. Many pathogens do not inflict any damage when the host grows under favourable conditions, but if weakened by other causes, then otherwise non-pathogenic organisms may inflict disease, as was observed for the usually non-pathogen *Armillaria gallica* damaging oak trees only if they had been weakened by powdery mildew (Marçais and Bréda 2006). Such pathogens are referred to as opportunistic pathogens (i.e., active only at the right opportunity). Synergistic interactions, where two or more pathogens together incite more damage than alone have been reported as well, especially between root-infecting nematodes (notably *Pratylenchus* and *Meloidogyne* spp.) and wilt-causing root pathogens (notably *Fusarium oxysporum* and *Verticillium dahliae*), but also between other taxa, e.g. fungi and chromists (Sanogo 2007).

An interesting phenomenon linked to multiple root pathogens (nematodes, fungi, chromists) relates to reduced performance of replanted fruit tree orchards (generally referred to a ‘replant disease’; Hoestra 1967; Mazzola and Manici 2012). In spite of much research, the etiology of this type of disease is not well-understood, probably because pathogen communities vary according to soil type, location, and plant species involved, and because the symptoms related to replant disease have also been observed in first year plantings. A range of root pathogens can occur in and on the fine roots of older trees, as was observed by Chavarriaga et al. (2007) for semi-natural and planted *Pinus sylvestris* in Scotland, including various *Pythium* spp. typically also isolated from orchard trees suffering from replant disease. Thus, replant disease could be caused by the resident root pathogens, which were enriched by the relatively large root systems of older trees, attacking young trees which likely were stressed shortly after planting. Pathogen enrichment in soils underneath older trees reducing the growth of conspecific seedlings has been observed also in a semi-natural forest for 7 out of 8 tree species studied (Yamazaki et al. 2009). Similarly Packer and Clay (2003) reported that *Pythium* spp. isolated from mature *Prunus serotina* incited mortality of conspecific seedlings, and suggested that this explained the usual large distance between trees in their native range in the U.S. Other examples of this intriguing phenomenon are mentioned by Burdon et al. (2006).

In agriculture, the role of root pathogens is different from that in natural vegetations (Table 6.2). Modern agroecosystems are characterized by rotation and fallow periods (favouring pathogens that can survive for a prolonged period in soil), by

Table 6.2 Key differences between managed vegetation (arable farming) and unmanaged vegetation (grassland, shrubland, forest) and their consequences for root pathogens

Item	Managed vegetation		Unmanaged vegetation	
	Description	Pathogens	Description	Pathogens
Plant diversity	Usually 1, occasionally 2 species, often annual	High rate of epidemics	Many, usually perennial	Low rate of epidemics
Gene pool of plants	Generally homogenous	Potentially high rate of epidemics	Heterogeneous	Low rate of epidemics
Rotation	Periods of fallow	Specialized resting structures needed	No periods of fallow	Survival in perennial roots possible; hence specialized resting structures not needed
Soil management	Strong soil disturbance (tillage), fertilization	Low opportunity for development of disease suppression	None	Relative good opportunity for development of disease suppression
Root pathogen composition	Usually one or a few dominant	High pathogen multiplication rate	Unknown, but probably more pathogens present	Low pathogen multiplication rate

high fertilization rates (enhancing root exudation and subsequent attack by root pathogens), and by genetic homogeneity of the crop (enhancing the rate of epidemics). On the other hand, unmanaged vegetations (grasslands, forests) are mostly dominated by perennial plants, enabling pathogen survival in living root systems. The role of root pathogens in unmanaged vegetations may remain more obscure than that in agroecosystems because once a plant has become weakened by a pathogen it may become outcompeted by other plant species well before it has been killed by the pathogen. In contrast, in monoculture agroecosystems, killed hosts are not replaced (or at best only in part by compensation of neighbouring plants). This reasoning is in line with a modelling study where it appeared that pathogen-affected agroecosystems are less stable than natural vegetations (Meyer et al. 2012). However, highly instable processes can occur in unmanaged vegetations if necrotrophic, bioinvasive pathogens are introduced. A famous example is the root fungal pathogen *Phytophthora cinnamomi* in Australia, which was probably introduced by humans early in the twentieth century (Cahill et al. 2008). This pathogen causes widespread death of many plant species including rare, endemic species.

Although the native range of most, if not all, root pathogens remains unknown, it seems likely that humans have contributed greatly to their dispersal (e.g. Atallah et al. 2012) and consequently at most locations root pathogens can be regarded as bioinvasive species. It seems that root pathogens typically found in arable systems have only little, if any activity in natural areas neighbouring these arable fields (although more research is needed to substantiate this); their massive occurrence is primarily explained by the high abundance and density of susceptible plants. In agroecosystems, suppression of root pathogens does occur, as soil sterilization followed by introduction of pathogens results in increased plant infection and disease compared to unsterilized soils (Weller et al. 2002). Disease suppression can be caused by aspecific (competition, fungistasis) and specific (hyperparasitism) mechanisms (Weller et al. 2002). In some pathosystems on some soils, spontaneous disease suppression has been observed (e.g. take-all decline caused by *Gaeumannomyces graminis* in e.g. wheat, Weller et al. 2002), but the successful introduction of the antagonists responsible for the phenomena into other fields has been shown to be difficult.

6.4.1 Managed Vegetations

Root pathogens have been studied most thoroughly in agriculture due to their great economic impact on crop yields. A primary reason for applying crop rotations (the alternation in time of crop species) is the general build-up of root pathogen populations during continuous cultivation of the same susceptible crop to yield-reducing levels (Bennett et al. 2012). Crop rotation is not self-evident: most modern farmers would prefer to specialize on a single, financially most beneficial crop. The build-up of root pathogen populations itself is a function of host growth, therefore build-up rate declines when yield loss increases, simply because there is less substrate for the

pathogen to colonize (e.g. Schomaker and Been 2006; Turner and Rowe 2006). At times that soils could be disinfested completely with methyl bromide, continuous cultivation of the same crop was common practice. However, nowadays soil disinfectants have been banned, and the use of more or less selective nematicides is becoming more restricted, while fungicides that control fungal root pathogens are rare. Choosing a crop rotation can be difficult if wide host range pathogens are present. Most wide host range root pathogens are limited to either monocotyledonous (e.g. *Fusarium culmorum*, *Striga hermonthica*) or dicotyledonous hosts (e.g. *Meloidogyne hapla*, *Verticillium dahliae*), but few can infect many hosts from both groups (e.g. *Meloidogyne chitwoodi*, *Macrophomina phaseolina*). With these wide host range pathogens also the choice of green manure crops (which are grown to reduce erosion and nitrogen leaching) and proper management of weeds on which pathogens can multiply is important (Sumner et al. 1995). In arable cropping, with its usual short periods of cultivation, it is no surprise that especially persistent pathogens are selected. Examples include *Synchytrium endobioticum* (causing potato wart disease and able to persist in the absence of a host longer than 20 years) and *Spongospora subterranea* f. sp. *subterranea* (powdery scab of potato; >20 years).

Root pathogens also infect perennial hosts, for example *Fusarium oxysporum* f. sp. *asparagi* in asparagus. Due to their nature, perennial crops or trees are somewhat less sensitive to root pathogens than annual plants, except in the case of some invasive pathogens (see below). Mechanisms of survival of perennial plants in the presence of root pathogens include presence of a physical layer of tissue that can be penetrated only when damaged (e.g. by machinery), abortion of infected tissue (by girdling of fine roots or by the formation of an impenetrable demarcation zone in wood, separating infected and non-infected host tissue), or growing towards uninfested soils (as is the case with planted dune grass species *Ammophila arenaria*, which is attacked by various root fungi and nematodes, and may temporarily escape by growing its roots towards pathogen-free blown-in sand (van der Putten et al. 1993)). Well-managed pastures generally have limited problems related to root pathogens. This is in sharp contrast with turf grasses, which suffer from a large array of root pathogenic fungi and nematodes, many of which are rare or unknown in pastures (Smiley et al. 2005).

Many agricultural root pathogens have a very wide distribution, with a major demarcation between the (sub) tropics and regions with more cool climates. Within these regions, many species are nearly ubiquitous, within the (sub) tropics for example *Striga hermonthica*, *Sclerotium rolfsii*, and tropical *Meloidogyne* spp. being very common, in the temperate regions for example *Verticillium dahliae*, *Pratylenchus penetrans*, and *Pythium* spp. being abundant and Mediterranean areas having both. As many of the root pathogens are lacking an airborne phase, one may wonder how they can be so ubiquitous. Clearly the transport of infected planting material is of utmost importance, as was exemplified by Atallah et al. (2012), who showed that the Californian genetic population structure of *Verticillium dahliae* affecting lettuce is heavily influenced by global trade. There are now many strict rules in the trade of this (see e.g. www.eppo.org), but in earlier times there was no awareness of these risks. On a regional scale it has been recognized that the dispersal of pathogens by machinery (within fields and from one infested field to another) is important.

Only a tiny amount of pathogen needs to arrive for successful settlement because of its persistence. Therefore, it is possible that dust storms can contribute to dispersal of strict soil-borne root pathogens, although this phenomenon has not been well investigated.

6.4.2 *Unmanaged Vegetations*

Except for habitats with primary successional stadia, the great majority of unmanaged vegetations is species-rich, with perennials (grasses, shrubs, trees) being common. The perennial nature of many plant species in unmanaged vegetations allows root pathogens to survive in living roots, in contrast to arable systems with annual crops. In species-rich vegetations a less evident role of root pathogens is to be expected than in arable systems because infected plants can be replaced by resistant or less susceptible plant species before they die. The role of root pathogens in unmanaged vegetations has been addressed only marginally, but their role is potentially large.

Empirically it can be hard to prove the role of root pathogens on vegetation production and composition. The mere presence of certain pathogens is a bad predictor of effects on certain plant species, as they depend on their density and conditions needed for successful pathogen development, including optimal soil temperature and soil moisture content, and low antagonistic activity. The influence of root pathogens is often deduced from increased plant growth after treatment of the soil with fungicides, but such results should be interpreted with care because of potential side-effects (e.g. increased availability of nutrients and effects on non-pathogenic organisms) and thus needs in any case a control soil that does not harbour the suspected pathogen(s). When comparing different soils, effects of plant available nutrients on plant production should be taken into account.

Overyielding of root biomass in species mixtures as compared to the sum of root biomass production in monocultures of the respective species has been observed repeatedly (Mommer et al. 2010; reviewed by de Kroon et al. 2012). After soil sterilization or fungicide treatment, root biomass in the monocultures increased to levels not unequal to that of the mixtures, suggesting a role of host-specific pathogens that act as function of host root density (Maron et al. 2011; Schnitzer et al. 2011). Also, pathogen-suppressive microorganisms enriched in specific rhizospheres could play a role, as it has been observed repeatedly that plant growth is less constrained if the soil is enriched with rhizosphere microorganisms from other plant species rather than from its own rhizosphere (reviewed by de Kroon et al. 2012).

Where pathogens limit the development of certain plant species, they leave space for other plant species, thus promoting vegetation diversity in space (e.g. Olff et al. 2000) or in time (van der Putten et al. 2005). In space, canopy gaps in forests have long been recognized as crucial elements for forest dynamics and diversity (Liu and Hytteborn 1991). In unmanaged *Pinus mugo* forests, canopy gaps appeared to be heavily infested with *Heterobasidion annosum* and *Armillaria ostoyae*, suggesting that they were the causing factors of these gaps (Bendel et al. 2006). Within this

context, Durrieu et al. (1985) referred to root pathogens as rejuvenating factors of forests. A time effect, i.e. succession, was shown for the early-successional dune grass *Ammophila arenaria* by later-successional plants, which was driven by appearance of species-specific plant pathogens (van der Putten et al. 1993). It has been stated that this can be true only if narrow host range pathogens are involved (Janzen 1970; Connell 1970), but similar mechanisms for wide host range pathogens are applicable as their quantitative effects on plant growth and development are usually strongly host species dependent (Augsburger and Wilkinson 2007). Being elsewhere bioinvasive weeds, in their native range *Centaurea macula* (spotted knapweed; Callaway et al. 2004), *Prunus serotina* (Reinhart et al. 2010; van der Putten et al. 2005) and *Ammophila arenaria* (Knevel et al. 2004) are maintained at low densities because of presence of root pathogens. Both wide and narrow host range pathogens seem to be implicated (Kliromonos 2002; Mills and Bever 1998; van der Putten et al. 2005). However, in explaining the dynamics of bioinvasive plants, release from airborne pests and pathogens can also be important (Allen et al. 2010; Blumenthal et al. 2009; Mordecai 2011; Mitchell and Power 2003; Mitchell et al. 2006; Torchin et al. 2003).

Seed pathogens are important drivers of seed decay in soil (Wagner and Mitschunas 2008). Their importance is usually shown by measuring seed germination incubated in fungicide-treated soils compared to untreated soils (Mitschunas et al. 2009). An array of fungi has been found to be associated with decaying seeds, including typical seed-borne fungi that have infected the seed aboveground, such as *Alternaria* spp., typical root pathogens such as *Cylindrocarpon* spp. and *Pythium* spp. (Schafer and Kotanen 2004), and opportunists such as *Penicillium* spp., that most likely are secondary pathogens. The effects of these organisms are strongly mediated by soil moisture content (Mordecai 2012). Three ecological groups of organisms that reduce populations of soil-incubated seeds have been recognized: (1) typical primary pathogens able to kill healthy seed under appropriate environmental conditions, (2) opportunistic pathogens that contribute to seed decline after its vitality has been negatively affected by other biotic or abiotic factors and (3) pathogens that kill the seed directly after germination. For the latter, Beckstead et al. (2007) found that there was a negative correlation between germination rate of seeds of *Bromus tectorum* and infection by the weak pathogen *Pyrenophora semeniperda*: so, rapid germination leads in this case to escape from the pathogen.

6.5 Conclusions

Root plant pathogens are important in agriculture, where they incite great losses, necessitating crop rotations, and in nature, where they shape vegetations in space (spatial heterogeneity) and time (succession). In arable farming, survival in the absence of a living host is crucial, whereas in perennial systems survival in host roots is possible. Some plants with bioinvasive properties appeared successful because of release from root pathogens present in their native range.

Ecological concepts on root pathogens have been developed mainly on the basis of agronomic damage they inflict. It is questionable to which extent these concepts can be applied to unmanaged systems. Compared to managed systems, unmanaged systems are usually species-rich, nutrient-poor, and multiple pathogens likely interact on different plants simultaneously. In perennial systems, survival on host roots could be more important than the survival in bare soil. As most root pathogens have a quite limited ability for dispersal, variation of pathogens (different species and different genotypes) in unmanaged vegetation likely plays a much larger role than in agricultural systems, where pathogens are dispersed through human action. The limited dispersal of root pathogens may also implicate that there are still many pathogens to discover in unmanaged systems. Especially the uncultivable root pathogens require more attention.

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Chapter 7

Non-trophic Interactions: Allelopathy

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Abstract Many plants release allelopathic chemical compounds into their surrounding that mediate allelopathic interactions. In natural ecosystems, these allelochemicals act indirectly by influencing abiotic components of the ecosystem, e.g., nutrient cycling, organic matter dynamics and soil nutrient availability, and can also alter biotic ecology by affecting soil microbes and plant pathogens. In managed ecosystems, allelopathy may directly affect other crops when grown in various management systems, through autotoxic effects, soil sickness or suppressing various weed and pest species. Thus allelopathy plays a significant role in the agroecosystems, forest plantations and agroforestry systems altering competitive interactions between plant species in the community and affecting crop yield. These interactions are mostly deleterious to the receiver plants but provide a selective advantage to the donor. The research and development of allelopathic research is of extreme importance for the improvement of agriculture, forestry and the global environment, because allelopathic interactions can also play a major role in the competitive success of invasive/exotic and native weeds, and allelopathic crops which disturb agricultural practices and cause environmental degradation. This chapter reviews the latest development in our understanding of allelopathy in promoting and restricting plant growth and the ways in which our knowledge can be used in sustainable management of natural and managed ecosystems.

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7.1 Introduction

In the first part of twentieth century, allelopathy research was focused mainly on agricultural productivity. However allelopathic patterns have been proven to occur in natural ecosystems, from boreal forests to tropical rain forests, from humid to desert ecosystems. In the last few decades, research of allelopathy has spread in agriculture, forestry and ecology both in natural and in managed ecosystems throughout the world (Chou 1999; Kohli et al. 2000, 2006; Inderjit et al. 2011; Macías et al. 2004; Muscolo and Sidari 2010; Putnam 1985; Rice 1984; Zeng et al. 2008; Narwal et al. 2011). Recently, studies of allelopathy in terrestrial systems have experienced tremendous development as interest has risen in describing biochemical mechanisms responsible for structuring plant communities, determining agricultural and forest productivity, and explaining invasive behaviors in introduced organisms (Cipollini et al. 2012; Mitrović et al. 2012).

Allelopathic interactions are based primarily on the production of secondary chemicals by higher plants that induce a wide array of biological changes, many of which we are still trying to understand (Macías et al. 2004). Although plant secondary metabolites are generally associated with plant defense responses against herbivores and pathogens, these compounds can be involved in a broad array of ecological functions at the ecosystem level, by influencing the community structure, nutrient dynamics, soil and mycorrhizal ecology and resource competition (Inderjit and Weiner 2001; Inderjit and Mallik 2002; Inderjit et al. 2011). Although the reduction of biodiversity is primarily a result of human activities perhaps a small number of plant species extinctions result from natural selection involving mechanism of plant interactions, such as allelopathy. In natural ecosystems, the most important influences of allelopathy occur through indirect effects rather than direct plant-plant interference (Inderjit and Weiner 2001), thus allelochemicals can influence abiotic components of the ecosystem, e.g., nutrient cycling, organic matter dynamics and soil nutrient availability. These chemicals can also alter biotic ecology by affecting soil microbes and plant pathogens. The abiotic environment (i.e. nutrient limitation, light regime and moisture deficiency) can in return influence the activities of the allelochemicals (Inderjit and Weiner 2001). In managed ecosystems, allelopathy may be effective in crops when grown in various management systems, as autotoxic effects, soil sickness or as suppressors of various weed and pest species (Kramer and Ben-Hammouda 2009). Recently, allelopathic research has focused on development of weed management strategies using allelopathic crop residues, with research interest in the mechanism of allelochemical action, and gene regulation of allelochemical production (Weston 2005). Likewise, allelopathic plants and their allelochemicals can be potentially utilized as an important part of pest management and control in agricultural ecosystems (Duke et al. 2000; Macías et al. 2004). In addition, recent studies have recognized allelopathy as an ecological mechanism of exotic plant invasion at the ecosystem level (Callaway et al. 2005). Thus the development of allelopathic research is of extreme importance for the improvement of agriculture, forestry and the global

environment (Zeng et al. 2008; Kohli et al. 2006). This chapter reviews the latest developments in our understanding of allelopathy in promoting and restricting plant growth and the ways in which our knowledge can be used in sustainable management of natural and managed ecosystems.

7.2 Effects of Allelopathic Chemicals on Plants and Microbes

Allelochemicals production is genetically regulated, and their concentration varies with age, cultivar, and plant organ; their amount is often enhanced by various biotic and abiotic stress factors. Pathogens, pests, parasites or herbivores can also stimulate allelochemical production. Thus any factor that induces stress can cause an increase in allelochemical production and release. Donor plants under stress often release a great variety and different concentration of allelochemicals, and stressed target plants may be more susceptible to allelochemicals (Reigosa and González 2006). Plant phytotoxins vary considerably in chemical structure, mode of action and effects (Bais et al. 2006).

Allelopathy has been defined as the term covering both detrimental and beneficial biochemical interactions among all classes of plants through the production of chemical compounds that are released into the environment (Rice 1984). Plants use a variety of mechanisms to release allelopathic compounds into their surrounding environment by volatilization, root exudation, leaching and decomposition of residues and thus reach the soil underneath the canopy.

7.2.1 *The Mode of Action*

The mode of action of the allelopathic compounds is often very subtle and difficult to determine correctly due to the limited means a plant has to express stress. The symptoms plants produce are often secondary in nature and difficult to diagnose (Chou 1999). Allelopathy interacts with plant stress, because stressed source plants often release a great variety and different concentration of allelochemicals, and stressed target plants may be more susceptible to allelochemicals (Reigosa and González 2006). To exert phytotoxic effects on other plant species, allelochemicals may have to move to the roots of the target plant through the soil. Once in the soil, they can affect soil chemistry i.e. nutrient cycling and organic matter dynamics, and change soil nutrient availability by either increasing or decreasing microbial activity (Castells 2008). Allelochemicals can decrease N availability by complexation with proteins from litter or with extracellular enzymes from microorganisms, thus delaying organic matter decomposition and mineralization (Hättenschwiler and Vitousek 2000; Wardle et al. 1998), by increasing microbial activity and N immobilization (Castells 2008) and by inhibiting fungal respiration and nitrification (Boufalas and Pellissier 1994). The resulting decrease in the inorganic N availability for plant

uptake may potentially affect plant growth. Therefore, soil fertility is influenced by allelopathic compounds from plant or microbial sources not only because they are important precursors of soil stable humic substances, but also for their effects on soil nutrient dynamics (N, P, K, Mn, Fe, Cu, etc.), pH, ion-uptake, soil aggregation, etc. (Muscolo et al. 2001; Muscolo and Sidari 2006; Djurdjević et al. 2010).

Allelopathy, as chemical modification of the site by an individual to enhance interference effectiveness, also involves ecological communications between species which can positively or negatively influence growth, behavior, reproduction, and survival of associated species (Narwal et al. 2000). Allelochemicals and other metabolites released by plant roots play important roles in rhizosphere signalling, plant defence and responses to abiotic stresses (Bais et al. 2006; Weston et al. 2012). Thus root exudates play a direct role in development of associations between parasitic plants and their hosts as well as indirect role in resource competition by altering the soil chemistry, soil processes and microbial populations (Bais et al. 2006). As a result, exudates can repel herbivores and microbes, stimulate symbiotic relationships, alter soil properties, and inhibit the growth of competing species (Mathesius and Watt 2011). Positive interactions between plants are sometimes controlled by root exudates due to the induction of defense responses in neighboring plants by reducing their susceptibility to pathogen infection or by initiating production and release of leaf volatiles that attract predators of plant enemies. In addition, effects of root exudates on soil processes and microbial populations can lead to some positive effects on neighboring plants e.g., Fe-mobilising phytosiderophores and phosphate-mobilising carboxylates that may lead to facilitation, i.e. amelioration of the environment of neighbouring plants (Lambers et al. 2008).

Allelopathic effects against higher plants are typically characterized as suppressing seed germination, root elongation and plant growth by inhibition of cell division. Several action modes have been observed, including direct inhibition of photosystem II (PSII) components, reduction in chlorophyll content, the reduction in CO₂ assimilation, interruption of dark respiration and ATP synthesis, and reactive oxygen species (ROS)-mediated allelopathic mechanisms (Barkosky and Einhellig 2003; Inderjit and Duke 2003; Weir et al. 2004; Djurdjević et al. 2008; Hussain et al. 2011). Another mode of action is the allelopathic effect on membrane permeability that causes an alteration in water and ion permeability of the cytoplasmic membrane (Yu and Matsui 1997). Allelochemical toxic effects frequently resulted in decreased stomatal conductance together with loss of leaf turgor (Yu et al. 2003), reduced leaf water potential, shoot turgor pressure, and osmotic potential (Barkosky and Einhellig 2003; Sánchez-Moreiras and Reigosa 2005). Disruption of plant water relations as the primary mechanism of the growth inhibition and the chronic reduction in available CO₂ and water stress are the possible causes for the reduction in photosynthetic efficiency (Fv/Fm) of PSII caused by allelochemicals. Other modes of action include disruption of mineral uptake and transport, inhibition of enzymatic activity, inhibition of germination and inhibition of seedling growth (Muscolo et al. 2001; Weir et al. 2004).

Allelopathy not only affects neighbouring plants and influences plant community structuring, but can also induce a broader ecosystem level change when it

coincides with disturbance (Wardle et al. 1998; Zackrisson et al. 1997). Allelopathic interactions are strongly tied to microbial activity in the soil, because soil microorganisms are both producers and degraders of allelochemicals and, at the same time, they can be affected by plant secondary metabolites (Pellissier and Souto 1999; Reigosa et al. 1999; Muscolo and Sidari 2006). From an ecological and evolutionary perspective, allelopathic effects of plants on soil microbes may have indirect effects on competing plants that are just as important as direct effects. Thus effects on the microbial community on which competing plants rely for nutrient and water uptake, nutrient cycling, and other interactions could promote growth of an allelopathic plant as long as it does not harm the microbial community in the process (Callaway and Ridenour 2004). From this perspective, soil microorganisms can be considered as allelopathic interaction regulators. This fact, pointed out by Blum (1995), is particularly relevant in forest ecosystems.

7.2.2 Role of Allelopathy in Promoting Plant Growth and Ecosystem Regeneration

Allelopathy has been studied mostly in the context of its effects on agricultural systems (Weston 2005), and its effects can be positive or negative in terms of crop establishment and performance (Weston and Duke 2003). However, researchers often ignored the stimulatory effects, possibly because stimulatory effects are often not as spectacular as inhibitory effects. There is evidence that allelochemicals, at certain concentrations, may be inhibitory but at lower concentrations; these allelochemicals might stimulate the growth of same or different species (Narwal et al. 2000).

Allelochemical compounds involved in allelopathic interactions are used by plants to counteract other plants, microorganisms, fungi, nematodes and insects (Michelsen et al. 1995). In earlier studies, in agriculture systems, numerous positive allelopathic effects were observed. For example, corn (*Zea mays* L.) residues increased grain yield of corn and soybean (*Glycine max* L. Merrill) (Crookston et al. 1991). Mughal (2000) found stimulatory allelopathic effect of leaf water extract of mulberry (*Morus alba* L.) on germination and seedling growth of peas (*Pisum sativum* L.), lentil (*Lens esculenta* Moench) and broad beans (*Vicia faba* L.), at concentration up to 50 %. In lentil crop, leaf leachate at 25 % water extract stimulated the germination and its seedling growth. Root exudates can have positive effects in plant-plant interactions, although these have been less frequently reported, by improving populations of certain soil microbes and reducing the others, resulting in a shift of nutrient accessibility and uptake by plants within the ecosystem (Inderjit and Weston 2003). Some root exudates induce defense responses in neighboring plants that reduce herbivore populations indirectly by attracting predators and parasites of the offending herbivore (Bais et al. 2006). For example, *V. faba* plants under attack release root exudates that induce green leaf volatile production in undamaged *V. faba* plants that in turn attracts aphid parasitoids (Du et al. 1998). Similarly, *Phaseolus lunatus* L.

plants under attack by spider mites produce root exudates that induce volatile production in undamaged *P. lunatus* plants, attracting predatory mites (Guerrieri et al. 2002). Leaf volatiles produced by plants under herbivore attack have also been shown to induce volatile production in neighboring plants, increasing the predator attraction signal (Bruin and Sabelis 2001).

Forestry can also benefit from allelopathy in weed control on valuable tree species (Chou 1986; Birkett et al. 2001). For example, reduction of raspberry (*Rubus idaeus* L.) development in a black spruce (*Picea mariana* (Mill.) B.S.P.) forests using a mulch of wheat, oat, barley or other donor plants is a good example of a new management technique (Mallik 1991). A number of wild plants and weed species are also reported to have antifungal activity against phytopathogenic fungi (Qasem 1996). Therefore, allelochemicals are one of the best environmentally sustainable methods of plant disease control. For example, allelochemicals released from the residues of allelopathic vegetable crops can greatly reduce the incidence of soil-borne pathogens. In addition, some root exudates that act as metal chelators in the rhizosphere can increase the availability of metallic soil micronutrients, including iron, manganese, copper, and zinc (Dakora and Phillips 2002). Metal chelators form complexes with soil metals, thus releasing metals that are bound to soil particles and increasing metal solubility and mobility. Finally, the ecological consequences of fire could be related to allelopathy as well. Only wildfires are able to reduce the presence of ericaceous shrubs and the allelochemical content in forest soil to levels which allow the successful regeneration of the tree canopy (Mallik 2003).

Stimulatory allelopathic effects of any plant on other plants can be used to develop ecofriendly, cheap, and effective growth promoters because the overuse of synthetic agrochemicals during last few decades often causes environmental hazards, an imbalance of soil microorganisms, nutrient deficiency, and change of soil physicochemical properties, resulting in a decrease of crop productivity. Although it is not possible to exclude use of synthetic herbicides completely at the present time their use can be reduced to a certain extent by utilizing allelopathic interactions as an alternative weed management strategy for crop production as well as environmental protection.

7.2.3 Role of Allelopathy in Restricting Plant Growth and Ecosystem Regeneration

The allelopathy describes direct or indirect effect of plant chemical compounds on another plant or other organism, although it is most often used to refer to chemical-mediated negative interference between plants (Chou 1999; Rice 1984; Narwal et al. 2000). Thus phytotoxic root exudates are generally associated with the reduction in neighbouring plant growth, and resistance to or suppression of plant pathogens, soil microbes, and other herbivores (Mohney et al. 2009). The use of allelopathic substances could inhibit the germination and seedling growth of crops and weeds (Weston 2005). Therefore, allelopathic crops may be used to effectively suppress

common and invasive weeds acting as new herbicides (Duke et al. 2000). Selective activity of tree allelochemicals on crops and other plants has also been reported. For example, *Leucaena leucocephala* (Lam.) de Wit, a tree promoted for revegetation, soil and water conservation and animal improvements in India, has deleterious effects on a number of other trees and crops (Chou and Kuo 1986).

7.3 Examples of Allelopathy in Managed and Natural Ecosystems

Allelopathy is receiving increasing attention because allelochemicals cause a number of ecological and economic problems, such as declines in crop yield due to soil sickness, replanting problems and regeneration failure of natural forests (Rice 1984; Inderjit and Duke 2003). This negative feedback has been seldom considered in natural ecosystems despite some early demonstrations of its existence (Florence 1965).

There is a variety of crop and weed species that establish some form of potent allelopathic interference, either with other crops or weeds, in agricultural settings, in the managed landscape or in naturalized settings. Release of allelochemicals from leaf residues or decomposing plant material is often a cause of natural regeneration deficiency in forests. Problems of natural regeneration, reforestation, and management are often ascribed to the presence of phenolic substances that may influence the growth of plants and the activities of soil microorganisms involved in the plant-soil system (Djurdjević et al. 2003, 2010; Mallik 2003).

Autotoxicity is ubiquitous in both natural and managed ecosystems and may have important ecological implications (Zeng et al. 2008). In agroecosystems, soil sickness occurs when the same crop or its related species are cultivated on the same soil successively (monocropping systems) and it seems to be generated by many factors: build-up of pests in the soil and disorder of physico-chemical properties of the soil (Jacob et al. 2006; Zeng et al. 2008). In forest ecosystems, soil sickness causes delaying and/or reducing seed germination and tree seedlings growth, autotoxicity, changes in soil microbial population structure and dynamics, reduced growth and respiration of mycorrhizal fungi, changes in soil nutrient dynamics, changes in decomposition process and forest regeneration failure (Dighton 2003).

Recent research suggests that allelopathic properties can render one species more invasive and thus potentially detrimental to both managed and naturalized systems (Callaway et al. 2005; Weston 2005). Exotic plant invasions often cause high mortality in native populations and therefore have the potential to be a powerful selective force. In contrast, the allelopathic crops have strong potential for the development of cultivars that are more highly weed suppressive in managed systems. A new challenge for plant scientists is to generate additional information on allelochemical mechanisms of release, selectivity and persistence, mode of action and genetic regulation, in order to protect plant biodiversity and enhance weed management strategies in a variety of ecosystems (Weston 2005).

7.3.1 *Managed Ecosystems*

Allelopathy plays a significant role in the agroecosystems, agroforestry systems and forest plantations leading to a wide array of interactions among crops, weeds and trees (Kohli et al. 2006). Generally, these interactions are deleterious to the receiver plants but may also provide a selective advantage to the donor. In mostly managed systems, during monoculture, homogenous metabolites and plant residues are accumulated in the soil, very often in high threshold levels, thereby leading to soil sickness (Jacob et al. 2006; Kohli et al. 2006) or autotoxicity when a plant species releases chemical substances that inhibit or delay germination and growth of members of that same species (Putnam 1985; Singh et al. 1999). The principal causes of crop autotoxicity include deliberately leaving crop residues or old roots in soil that release phytotoxins which may directly affect success, cause microbial imbalance, change organic matter of soil, increase ion leakage, disturb nutrient uptake and immobilization (Yu and Matsui 1997). Crop autotoxicity is particularly acute in croplands where tillage is not practiced. In the phenomenon of soil sickness, the release of substances during the decay of dead plant residues plays a role greater than the active secretion of allelochemicals by plants (Polyticka 2005).

7.3.1.1 *Phytotoxicity and Soil Sickness*

In both cereal and vegetable crops, it has been noted that a significant reduction in yield and quality is due to natural soil sickness. Some very important crops expressed autotoxicity and heterotoxicity, including rice, wheat, maize, sugarcane, alfalfa and vegetable crops like, cucumber, tomato, pea, etc. (Table 7.1.). For example, flavonoids from sunflower have suppressive effects on root and shoot length of lettuce (*Lactuca sativa* var. *nigra*), cress (*Lepidium sativum* L.), tomato (*Lycopersicon esculentum* Mill.) and barley (*Hordeum vulgare* L.) seedlings (Maciás et al. 1996). Inhibitory effects of leaf extract and residues of sunflower to wheat, maize, sorghum, soybean, winter wheat and sunflower itself were observed for germination and seedlings growth (Batish et al. 2002; Kohli et al. 1998). Reduced germination and seedling establishment was observed in both sunflower and cotton crops planted after sunflower (Narwal 1999). It was also found that wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), oats (*Avena sativa* L.) and rice (*Oryza sativa* L.) extracts significantly reduced root growth of alfalfa (*Medicago sativa* L.) (Chon and Kim 2004). Rice inhibited root and seedlings growth of duck salad (*Heteranthera limosa* and *Lactuca sativa* L.) (Ebana et al. 2001; Kato-Noguchi et al. 2008).

Monocropping of the legume, mungbean (*Vigna radiata* L.), for many years on the same field causes up to 25 % plant growth inhibition of lettuce (Chou 1995). Allelopathic inhibition of a number of turnip species e.g., *Brassica nigra* L. on alfalfa, wheat and radish was also seen (Turk et al. 2003, 2005). Likewise, brassica species have harmful effects on other crops by reducing seed germination and emergence of subsequent small-grain crops when grown in rotation (Bialy et al. 1990).

Table 7.1 Phytotoxic crop species (autotoxic and heterotoxic) and their allelochemicals

Autotoxic species	Heterotoxic species	Allelochemicals
Rice (<i>Oryza sativa</i> L.)	Rice (<i>Oryza sativa</i>)	Phenolic acids: <i>p</i> -hydroxybenzoic, vanillic, <i>p</i> -coumaric, syringic, ferulic
Wheat (<i>Triticum aestivum</i> L.)	Wheat (<i>Triticum aestivum</i> L.)	Hydroxamic acids: 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) Phenolic acids: <i>p</i> -coumaric, syringic, ferulic acids, <i>p</i> -hydroxybenzoic, vanillic, <i>cis-p</i> -coumaric, <i>cis</i> -ferulic, <i>trans-p</i> -coumaric, <i>trans</i> -ferulic
Sunflower (<i>Helianthus annuus</i> L.)	Sunflower (<i>Helianthus annuus</i> L.)	Sundiversifolide, 4, 15-dinor-3-hydroxy-1(5)-xanthene-12, 8-olide
Maize (<i>Zea mays</i> L.)	Maize (<i>Zea mays</i> L.)	Hydroxamic acids: 5-chloro-6-methoxy-2-benzoxazolinone (C118 MBOA), 6-methoxy-2-benzoxazolinone (MBOA) and 2, 4-dihydroxy-1, 4-benzoxazin-3-one (DIBOA) Phenolic acids: <i>p</i> -hydroxybenzoic, vanillic, ferulic, <i>o</i> -coumaric, <i>o</i> -hydroxyphenylacetic, salicylic, syringic, <i>p</i> -coumaric, transcinnamic, caffeic acids
Cucumber (<i>Cucumis sativa</i> L.)		Phenolic acids: Benzoic Cinnamic
Mungbean (<i>Vigna radiata</i> L.)	Sugarcane (<i>Saccharum officinarum</i> L.) Mustard (<i>Brassica nigra</i> L.) Mulberry (<i>Morus alba</i> L.) Barley (<i>Hordeum vulgare</i> L.) Oats (<i>Avena sativa</i> L.)	

Autotoxicity has been observed also in the garden asparagus (*Asparagus officinalis*) and garden cucumber (*Cucumis sativa*) (Yu et al. 2003). Mulberry (*Morus alba* L.) is an allelopathic plant where inhibitory effects of its fallen leaves on the understorey vegetation have also been noticed. Mughal (2000) found allelopathic effect of leaf water extract of *M. alba* on germination and seedling growth of peas, lentil and broad beans.

Allelochemicals have mostly negative effects on crop plants such as inhibition of nitrification and biological nitrogen fixation, (ii) predisposing the plants to diseases and (iii) inhibition or stimulation of germination, growth and yield (Hicks et al. 1988).

7.3.1.2 Allelopathic Crops

It was found that cover crop residues present on the soil surface suppress weeds physically and when allelochemicals released during decomposition of these residues also give selective weed control (Putnam 1985; Weston 1996). In recent studies, intercropping that provides better weed suppression through resource competition/ or allelochemical exudation into the rhizosphere has been addressed as an option for integrated weed management (Iqbal et al. 2009). The most frequent allelopathic crops and their effects in suppressing growth of weeds are listed in Table 7.2.

In earlier studies, it was found that growing wheat or mulching with wheat straw can effectively control weeds in fields and orchards. Thus growing allelopathic wheat varieties significantly decreased weed infestation in the field and reduced the weed biomass in the following crops (Kong et al. 2007). Similarly, rice is an allelopathic plant and many studies on rice cultivars as a means of ecological weed control strategy have been presented (Rimando et al. 2001). For example, rice inhibited germination, seedling growth and root length of weeds *Parthenium hysterophorus* L. (Javaid et al. 2006) and Chinese milk vetch (*Astragalus sinicus* L.) (Pramanik et al. 2001). The allelopathic effect of rice was also found on *Sagittaria montevidensis* Cham. & Schltdl. root growth (Seal et al. 2004), *Echinochloa crus-galli* (L.) P. Beauv. and *Heteranthera limosa* (Sw.) Wild. (Kato-Noguchi 2011; Ebana et al. 2001). Soil incorporation of rice residues reduced the population of both broadleaved and grassy weeds (Narwal et al. 2000). Straw and hulls of some rice cultivars suppressed the germination of *Echinochloa crus-galli* and mustard (Ahn and Chung 2000). Therefore, allelopathic rice plants through inhibitory effects on weeds as developed with genetic alterations in rice cultivars can lower production costs by reducing herbicide application and could benefit farmers, consumers as well as the environment (Rimando et al. 2001). Although maize (*Zea mays* L.) is an allelopathic plant, it gained less attention than allelopathy in rice or wheat. Allelopathic compounds from rice were found inhibitory to roots growth post harvest in weed seedlings like *Lepidium sativum* L. (Kato-Noguchi et al. 2008). Likewise, the cultivated sunflower (*Helianthus annuus* L.) is an economically important oil seed crop, and some studies indicate that sunflower root, stem and leaf extracts caused significant reduction in dry weight of *Phalaris minor* Retz., *Chenopodium album* L. *Coronopsis didymus* L. Smith, *Rumex dentatus* L. *Parthenium hysterophorus* L. and *Medicago polymorpha* L. (Javaid et al. 2006).

Sorghum (*Sorghum bicolor* L.) also contains a number of allelochemicals that possess phytotoxic effect against weeds. Previously, Panasiuk et al. (1986) revealed that weeds such as *Echinochloa crus-galli* (L.) Beauv., *Amaranthus retroflexus* L. and *Rumex acetosella* L., when interplanted with sorghum showed a significant reduction in their germination, growth and dry weight. Later, Cheema and Khaliq (2000) revealed that water extracts of mature sorghum plants reduced the weed density and weed biomass by 35–49 %. For example, seed germination and root length of weed *P. hysterophorus* L. was significantly reduced by extracts of sorghum (Javaid et al. 2006). Cultivated or naturally occurring *Brassica* spp. has been reported to be weed suppressive for many years (Siemens et al. 2002). Narwal

Table 7.2 Allelopathic crops with potential for weed suppression

Allelopathic crop	Weed	Allelochemicals
Wheat (<i>Triticum aestivum</i> L.)	<i>Echinochloa crusgalli</i> L. Beauv <i>Ipomoea hederacea</i> Jacq	Hydroxamic acid: 2,4-dihydroxy-7-methoxy-1, 4-benzoxazin-3-one (DIMBOA)
Rice (<i>Oryza sativa</i> L.)	<i>Parthenium hysterophorus</i> L. <i>Astragalus sinicus</i> L. <i>Sagittaria montevidensis</i> Cham. & Schl. <i>Heteranthera limosa</i> (Sw.) wild. <i>Lactuca sativa</i> L. <i>Echinochloa oryzicola</i> Vasing. <i>Monochoria vaginalis</i> Presl var. <i>plantaginea</i> Solms-Laub.	Phenolic acids: <i>p</i> -hydroxybenzoic, vanillic, <i>p</i> -coumaric, syringic, ferulic acid
Maize (<i>Zea mays</i> L.)	<i>Lepidium sativum</i> L. <i>Avena sativa</i> L. <i>Phleum pretense</i> L. <i>Digitaria sanguinalis</i> L. <i>Lolium multiflorum</i> Lam. <i>Amaranthus caudatus</i> L. <i>Chenopodium album</i> L. <i>Amaranthus retroflexus</i> L.	Hydroxamic acids: -chloro-6-methoxy-2-benzoxazolinone (C18 MBOA), 6-methoxy-2-benzoxazolinone (MBOA), 2, 4-dihydroxy-1, 4-benzoxazin-3-one (DIBOA)
Sunflower (<i>Helianthus annuus</i> L.)	<i>Synapis arvensis</i> L. <i>Abutilon theophrasti</i> L. <i>Datura stramonium</i> L. <i>Ipomoea hederacea</i> Jacq <i>Amaranthus retroflexus</i> L. <i>Phalaris minor</i> Retz. <i>Chenopodium album</i> L. <i>Coronopsis didymus</i> (L.) Sm. <i>Rumex dentatus</i> L. <i>Medicago polymorpha</i> L. <i>Parthenium hysterophorus</i> L. <i>Orobancha cernua</i> L. <i>Chenopodium album</i> L. <i>Rumex dentatus</i> L.	Phenolic acids: chlorogenic, caffeic, vanillic, syringic, ferulic
Sorghum (<i>Sorghum bicolor</i> L.)	<i>Echinochloa crus-galli</i> (L.) Beauv. <i>Amaranthus retroflexus</i> L. <i>Rumex acetosella</i> L. <i>Parthenium hysterophorus</i> L.	Phenolic acids: benzoic acid, <i>p</i> -hydroxybenzoic, vanillic, <i>m</i> -coumaric, <i>p</i> -coumaric, gallic, caffeic acid, ferulic and chlorogenic acid, sorgoleone
Brassica spp.	<i>Physalis angulata</i> L. <i>Phalaris minor</i> Retz. <i>Avena ludoviciana</i> Durieu <i>Cirsium arvense</i> (L.) Scop. <i>Chenopodium album</i> L. <i>Melilotus alba</i> Medik. <i>Rumex retroflexus</i> L.	Benzoyl, o-tolyl, m-tolyl, tert-octyl, 3-fluorophenyl

(1994) found that some accessions of *B. juncea* and *B. nigra* caused significant reduction of 75–98 % in the density of winter weeds *Phalaris minor* Retz., *Avena ludoviciana* Durand., *Cirsium arvense* (L.) Scop., *Chenopodium album*, *Melilotus alba* and *Rumex retroflexus*, respectively. Allelopathic effect of aqueous extracts of perennial legumes (*Mucuna deeringiana* (Bort) Merr., *Canavalia ensiformis* (L.) DC., *Leucaena leucocephala* (Lam.) de Wit and *Lysiloma latisiliquum* (L.) Benth.) was shown to be efficient in suppression for growth of *Echinochloa crusgalli* L. P. Beauv., and *Amaranthus hypochondriacus* L. (John and Narwal 2003). The use of mulberry (*Morus alba* L.) might be useful option for biological weed control and for the reduction of herbicides use in paddy field agriculture due to suppression of weed population in rice by 72.7 % and promotion of rice paddy yield by 23.3 % (Hong et al. 2003).

Putnam and Duke (1974) first introduced the concept of using allelopathic crops to suppress weed growth in agriculture, as they mentioned the weed-suppressive crops and their effectiveness for use in weed management. Later research efforts have made it possible to use allelopathy for increasing crop production, to reduce reliance on synthetic pesticides and improve environmental health (Qasem and Foy 2001; Rice 1984; Weston 1996). Therefore, the current trends in agriculture production are to find a biological solution to reduce the apparent harmful impacts from herbicides and pesticides.

7.3.1.3 Agroforestry Systems

In addition to crops, trees are also an integral part of the agriculture under various intensive and extensive agroforestry systems. Agroforestry is a modern tool to develop sustainable land use and to increase food production by growing woody species with agricultural crops and/or animals; however negative allelopathic effects have also been recognized (Kohli et al. 2000). In this situation, multiple plant species can coexist with the agricultural crops, thus their allelopathic compatibility may be crucial to determine the success of an agroforestry system. As tree species remain a part of the agroecosystem for a longer period, and most of them produce a large amount of leaves and litter, their allelochemicals may play an important role in developing an eco-friendly pest management strategy.

A significant reduction in crop density, root and shoot length and biomass were observed due to allelopathic effect of *Eucalyptus* spp. Trees, for example, *Eucalyptus camaldulensis* Dehnh. causes meristematic root tips and radical growth, and peroxidase activity in *Lepidium sativum*, *Rumex acetosella*, and *Avena fatua* L. in Iran (Moradshahi et al. 2003). *Eucalyptus citriodora* Hook. caused inhibition of *Avena fatua* and amaryllis (*Hippeastrum hybridum* Hort.) in Egypt (El-Rokiek and Eid 2009). *Eucalyptus dundasii* Maiden. inhibited germination and growth of *Lolium rigidum* Gaudin and *Hordeum glaucum* L. in Australia too (Wu et al. 2011) while *Eucalyptus tereticornis* Sm. reduced seedling growth and photosynthesis of *Amaranthus viridis* (Kaur et al. 2011) in India. Effect of *Gliricidia sepium* litter reduced survival of kans grass *Saccharum spontaneum* L. (Cumplings et al. 2012). Likewise, various species of

Table 7.3 Allelopathic trees and their effects on crops and other plants

Tree species	Response species	Allelopathic effects on crops
<i>Acacia</i> spp.	<i>Hedera hibernica</i> G. Kirchn. <i>Dactylis glomerata</i> L.	Affected net photosynthesis and respiration
<i>Albizia lebbbeck</i> (L.) Benth.	<i>Lactuca sativa</i> L.	Inhibition of germination and growth
<i>Eucalyptus</i> spp.	<i>Lepidium sativum</i> L. <i>Rumex acetosella</i> L. <i>Avena fatua</i> L. <i>Lolium rigidum</i> Gaudin <i>Hordeum murinum</i> L. ssp. <i>glaucum</i> (Steudel) Tzvelev	Reduction of crop density, root and shoot length and biomass Inhibition of meristematic root tips and radical growth, and peroxidase activity
<i>Juglans</i> spp.	<i>Sinapis alba</i> L. <i>Zea mays</i> L. <i>Glicine max</i> (L.) Merr.	Inhibition of germination and growth
<i>Leucaena leucocephala</i> (Lam.) de Wit	<i>Sorghum</i> spp. <i>Vigna unguiculata</i> (L.) Walp. <i>Helianthus annuus</i> L.	Reduction of growth and development of crops
<i>Populus deltoides</i> W. Bartram ex Marshall	<i>Triticum aestivum</i> L. <i>Lens culinaris</i> Medikus <i>Phaseolus mungo</i> (L.) Hepper <i>Avena sativa</i> L. <i>Trifolium alexandrinum</i> L. <i>Brassica juncea</i> (L.) Czern. <i>Helianthus annuus</i> L.	Loss of yield

Populus, *P. deltoides* especially, are also known to exert allelopathic effect on other plants including crop plants (Kohli et al. 2000) due to the toxicity of allelochemicals including phenolic acid and salicin. *Leucaena leucocephala* is another fast growing nitrogen-fixing multipurpose tree that has been widely used under various agroforestry plantations. Its leaf and litter aqueous extracts have inhibitory effects on a number of plant species including crops like sorghum, cowpea and sunflower (Singh et al. 2001). *Albizia lebbbeck* (L.) Benth. can also inhibit germination and growth of mungbean and soybean (Parvin et al. 2011). The most frequent allelopathic trees and their effects in suppressing growth of crops are listed in Table 7.3.

Studies with various tree and shrub plants can be used for further applications of allelopathy in weed control. Therefore, if properly understood and the nature of chemicals involved is elucidated, such mechanisms can be effectively exploited to enhance crop productivity through management of weeds, nematodes, pathogens and insects. Agroforestry can, therefore, be manipulated to make agroecosystems sustainable through proper management and/or mulching of the litter of the trees growing in agroecosystems to improve the soil quality, conserve moisture and bring about the cooling effect (Kohli et al. 2006).

7.3.1.4 Forest Ecosystems

Although the study of allelopathy involving plants in agricultural and horticultural systems has a long history of allelopathy, research in forested ecosystems is rather recent (Mallik 2008). In such ecosystems the soil plays an important role as the matrix through which potential allelochemicals pass, therefore, the influence of allelochemicals on different components of the soil ecosystem and their role in shaping community structure has been studied by numerous authors (Rice 1984; Einhellig 1995; Boufalas and Pellissier 1994; Inderjit and Mallik 1997; Djurdjević et al. 2004, 2010; Muscolo and Sidari 2010; Mitrović et al. 2012; Pavlović et al. 2013; Wardle et al. 1998). Allelopathic effects are directly related to forestry issues, for example the delay and reduction of germination, and/or stunted growth of conifer tree seedlings by allelopathic activity of the understory species (Mallik 2003; Pellissier and Souto 1999). Shrub species often quickly invade areas disturbed by removal of canopy trees by forest harvesting due to their stress tolerating strategies and form a dense understory that can alter natural regeneration of trees (Mallik and Prescott 2001). Therefore, one of the greatest challenges for plant ecophysiologists today is restoring natural and crop forests.

In forestry systems, allelopathy can affect many aspects of plant ecology including occurrence, growth and plant succession, the structure of plant communities, dominance, diversity and plant productivity. The allelochemicals released from forest trees affect the understory species, at least affect the donor species and may cause problems of natural regeneration in forest ecosystems (Reigosa et al. 2000; Djurdjević et al. 2003). In forest plantations there are generally one or few dominant tree species, which would lead to accumulation of allelochemicals of these species. The intensive modern forestry has led to serious changes in the physico-chemical and biological properties of soil. Effect of soil sickness can be observed better in ecosystems which are affected by anthropogenic activities, mainly in replacing natural mixed forests by monocultures. Thus forestry continuous monoculture slowly intoxicates the soil, leading to the gradual changes in stand structure and tree species composition (Caboun 2005). In such case, soil sickness appears to be widespread. Allelopathic effects of certain canopy trees on tree seedlings and understory plants have direct effects on forest regeneration (Mallik 2008). In addition, introduction of exotic tree species in forest plantation may also increase accumulation of allelochemicals in soil due to very high requirements of such species for water and nutrients and consequently cause their deficit in soil, leading to increased production of allelochemicals. In addition, the soil microflora, as important mediators of allelopathy, may not be adapted to such allelochemicals, which leads to its accumulation in toxic levels in soil.

Most forests are managed for timber production. In such forests the fate of natural understory plant communities, and thus of plant diversity in general, is a function of silvicultural practices, that promote rapid decomposition of plant material, designed with the primary intent of maximizing the value of the dominant tree crop (Roth et al. 2002). Silvicultural practices change the physico-chemical conditions of the soil or the biotic relations into the soil solution (Leckie et al. 2004) and therefore, change the allelopathic tree-understory relationships. However, the establishment and productivity decline of replanted tree ecosystems has remained a significant

problem. Autotoxicity is a major reason for managed tree ecosystems regeneration failure, causing replant problems. Thus, *Eucalyptus exserta* F. Muell. and *Eucalyptus urophylla* S.T. Blake were introduced in 1960s and become dominant species in man-made forest communities in South China to supply the paper industry. However, aqueous leaf leachate and leaf volatile of *E. urophylla* expressed allelopathic effects on several native tree species including *Cinnamomum burmanni* (C. Nees & T. Nees) C. Nees ex Blume, *Cryptocarya concinna* Hance, *Machilus chinensis* (Benth.) Hemsl., *Photinia benthamiana* Hance and *Pygeum topengii* Merr. (Fang et al. 2009).

In fire adapted boreal forests, particularly natural fires, the level and distribution of fire severity play a critical role in the manifestation of forest allelopathy. The high severity fires break down allelochemicals by thermal decomposition, create favorable seedbed by consuming forest floor humus and releasing nutrients and removing competing plants by killing underground regenerating structures. Clearcut harvesting and low-severity fires on the other hand, may promote vegetative regeneration of understory plants with competitive and allelopathic properties as their underground perennating structures remain unharmed. This may cause retrogressive succession by resisting tree colonization and inducing long-term habitat degradation (Mallik 2008).

Control of competing and allelopathic plants by herbicides after forest harvesting is a serious issue in forestry. Alternative methods such as use of allelopathic straw mulch, herbicides of biological origin, planting tree seedling pre-inoculated with mycorrhiza, and scarification and spot fertilization at planting have produced good results. It is possible to develop alternative methods of weed control in forestry by using allelopathy.

7.3.2 Natural Ecosystems

The idea of allelopathy as an ecological phenomenon structuring natural plant communities is rather recent (Mallik 2005). Unlike managed systems, allelopathic effects can result from interactive effects among multiple compounds (Inderjit et al. 2011) thus making it difficult to consistently demonstrate allelopathy in natural conditions and to identify the ecological relevance of particular chemicals. Belowground influences of ecosystem processes driven by soil biota, genetic effects on root interactions, and complex interactions among different root exudates seem to shape allelopathic interactions (Blair et al. 2006).

7.3.2.1 Population and Community Structure Changes by Invasive Species

Research of allelopathic activity in natural ecosystems has often been initialised by field observations of changes in vegetation patterns in natural habitats such as reduced species richness. In Spanish scrublands, the floristic diversity of other species has been reduced by *Cistus ladanifer* L. allelochemicals that inhibited or delayed germination, and reduced seedling growth of species that are growing adjacent to

C. ladanifer scrublands. Thus the distribution of these species is apparently limited by the allelopathic action of *C. ladanifer* (Chaves and Escudero 1997). The release of allelochemical compounds from *Ailanthus altissima* (P. Mill.) Swingle also has inhibitory effects on neighbouring plant species (Gómez-Aparicio and Canham 2008). Likewise, Mallik and Pellissier (2000) found that the Eurasian *Vaccinium myrtillus* L. generally showed stronger biochemical affects on the North American *Picea mariana* than on the Eurasian *Picea abies* (L.) Karst. Similarly, exotic invasive woody weed *Lantana camara* L. that form dominant components within various types of Australian forests was shown to interrupt natural forest regeneration processes by decreasing germination, reducing early growth rates, and reducing survival of natural species (Gentle and Duggin 1997). Another example is the allelopathic tree *Acacia dealbata* Link, an Australian woody legume, that has become a serious environmental problem in Northwest Spain, where its expansion is assumed to reduce populations of native species and threaten local plant biodiversity (Lorenzo et al. 2011).

Exotic plant invasions often cause high mortality in native populations. A few examples demonstrate the importance of allelopathy for successful invasion e.g. two of North America's most destructive invaders, *Centaurea maculosa* auct. Amer., and *C. diffusa* Lam. that establish virtual monocultures and both species have powerful antiplant and antimicrobial root exudates (Callaway et al. 2005). *Alliaria petiolata* (M. Bieb.) Cavara & Grande, a devastating invader of North American temperate forests, also has strong allelopathic effects on *Geum laciniatum* Murray and *Geum urbanum* L. (Prati and Bosdorf 2004). The release of allelochemicals from plants known as aggressive colonisers *Elytrigia repens* (L.) Gould and *Vulpia myuros* (L.) C.C. Gmel., suggests that allelopathy is often involved in successful invasions (An et al. 1997). In New Zealand, allelochemicals from decomposing leaves of *Carduus nutans* L. have been reported to be involved in the establishment of this species in pastures of *Lolium perenne* L. and *Trifolium repens* L. (Wardle et al. 1998). The decline in soil nitrogen input may benefit the subsequent *C. nutans* cohorts as this species tolerate low nitrogen conditions better than most forage species that illustrates how the allelopathic activity of a plant species may contribute to changes in ecosystem functioning, particularly N fixation (Wardle et al. 1998).

Weidenhamer et al. (1989) suggested that the allelopathic effect might be intensified in natural communities where overall plant densities are lower for example because of stressful environmental conditions e.g. communities such as the Florida scrub, the California coastal chaparral and dry tropical scrub communities. Allelopathy is also more intensive in poor soils (Inderjit and Callaway 2003) supporting the hypothesis that allelopathy increases the invasive potential of exotic plants in environments with low resource availability (Hiero and Callaway 2003). Such a statement partially explains how some plants become invasive monotypes in their area of introduction (Ridenour and Callaway 2001).

Allelopathy is a natural process also present in forest ecosystems that strongly influences forest development. Namely, stress or exotic species invasion could increase allelopathic importance in many forests. There are reports about allelochemical production in many woody species, from *Eucalyptus* sp. forests in Australia (Lovett 1986), to boreal conifer forests (Mallik 2003), tropical forests

(McKey et al. 1978), temperate forests (Willianson et al. 1992) and sub-desert communities (Van Rooyen et al. 2004). Conifer forests with ericaceous understory or *Eucalyptus* sp. forests are ecosystems with a strong allelopathic influence. Most studies dealing with allelopathy were focused on the allelochemical influence on conifer forest regeneration following disturbances such as wildfires, windstorms or clearcuts (Pellissier and Souto 1999). In Canada and northern Europe, ericaceous shrubs proliferate during the period of higher resource availability after tree canopy removal and then allelochemical production and accumulation in forest soil increases (Mallik 2003). The conifer seedlings, the most allelochemical-susceptible stage, are not able to compete with ericaceous plants and their ability to develop mycorrhizae is inhibited (Inderjit and Mallik 2002). Numerous negative allelopathic effects were reported for understory phenolic-containing associated shrubs (*Ledum palustre* L. and *Empetrum hermaphroditum* L.), inhibitory effects on seed germination, rooting ability, seedling growth and regeneration of spruce species (*Picea glauca* (Moench) Voss and *Picea mariana* (Mill.) Britton, Sterns & Poggenb.) (Castells et al. 2005) and inhibition of *Pinus sylvestris* L. regeneration post-fire in sites dominated by *E. hermaphroditum* (Zackrisson et al. 1997), and suppression of vascular plant growth in Sphagnum-dominated bogs. In another example, secondary metabolites from *E. hermaphroditum* inhibited symbiotic associations between *P. sylvestris* trees and mycorrhizal fungi, thus reducing *P. sylvestris* nitrogen uptake (Nilsson and Zackrisson 1992). Moreover, secondary metabolites in *E. hermaphroditum* litter inhibit soil microbial and macrofaunal activity, thus reducing decomposition rates and further reducing soil nutrient availability (Wardle and Lavelle 1997). The allelochemicals from ericaceous *Kalmia angustifolia* L. affect root growth of *P. mariana* (Inderjit and Mallik 2002). Only wildfires are able to reduce the presence of ericaceous shrubs and the allelochemical content in forest soil to levels which allow the successful regeneration of the tree canopy (Mallik 2003). Changes in the mineralization and decomposition rates, as the main factors responsible for the changes in humus characteristics following a *K. angustifolia* invasion, may be the cause of changes in soil fertility (Yamasaki et al. 1998). Similar relationships have been reported in *Cryptomeria japonica* (L. f.) D. Don forests in Taiwan (Chou 1986) and in *Eucalyptus* sp. forests in Australia (Lovett 1986).

In natural forest ecosystems the concentration of allelopathic compounds in the surrounding environment are variable and can be seasonally based. Allelochemicals released from the tree bark, needles, litter and root/mycorrhizal exudates remain in the soil and interfere with the germination of seeds or growth and development of young seedlings thus preventing their natural regeneration. Fernandez et al. (2006) and Monnier et al. (2011) reported an autotoxicity due to the allelopathy as the main reason for natural regeneration failure in the fire free *Pinus halepensis* Mill., forest in the Mediterranean basin. Allelochemicals are released by trees for a long period, and during time they may accumulate in soil to toxic levels. Some examples of strong allelopathic effects can be found in the genus *Acacia*, *Ailanthus*, *Eucalyptus*, *Juglans*, *Leucaena* and some *Quercus* species (Cummings et al. 2012; Lorenzo et al. 2011; Hussain et al. 2011). Inhibition of germination and retardation of seedlings are the most common allelopathic effects in natural ecosystems.

7.4 Conclusion

Environmental implications of allelochemical compounds are difficult to quantify and evaluate in both natural and managed ecosystems due to numerous confounding factors. In addition, the interactive nature of allelopathic compounds and occurrence of multi stresses under field conditions further complicates the problem. Beside natural environmental change, plants cope with a variety of increased human-induced environmental changes during the last decades. Thus, allelopathy is receiving increasing attention because allelopathic interactions among crops, weeds, trees and microbes play an important role in the managed ecosystems thereby resulting in a decline in crop productivity, problem of soil sickness, increasing depletion of biodiversity and regeneration failure of natural forests. Therefore, there are two major challenges for researchers to minimize the negative impacts of allelopathy on crop growth and yield and to exploit allelopathic mechanisms as additional pest control or crop growth regulation strategies. Allelochemicals and/or their derivatives can directly be used as novel chemicals for sustainable management in an ecofriendly manner.

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Chapter 8

Viruses in Soil

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Abstract It has become apparent in recent years that the diversity of viruses in the environment is much greater than that inferred from known viruses which are predominately pathogens of humans and of organisms important to man. Soils could contain in excess of 10^8 virus particles/gram of soil and this wide variety of viruses can affect plant growth in many different ways. Soil-borne viruses that are pathogens of plants can have obvious deleterious effects. These plant viruses can exist either freely or in association with soil-inhabiting vector organisms such as nematodes or other microorganisms. Other viruses can infect microorganisms in the soil and thus affect soil microbial functioning. Viral pathogenesis of soil microorganisms can have obvious positive or negative effects depending on whether the affected microorganism is beneficial or deleterious to plant growth. Another consideration is that viral pathogenesis of soil microorganisms can contribute to recycling of nutrients within soil microbial populations. An important effect that viruses can have on microbial populations is by mediating horizontal gene transfer and metagenomic approaches are beginning to give an understanding of potentially how widespread and important this process may be in facilitating the responses of microbial populations to environmental changes.

8.1 Introduction

Viruses are the most abundant biological entities on our planet and exceed the number of cellular organisms in marine and soil habitats by at least an order of magnitude (Suttle 2005; Edwards and Rohwer 2005; Casas and Rohwer 2007). The global

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population size of viruses is estimated to be $>10^{30}$ virus particles (Chibani-Chennoufi et al. 2004) and analysis of the viruses in a 1 kg sample of marine sediment indicated that there was greater diversity in that population than in all the amphibians or reptiles on the planet (Breitbart et al. 2004a). The concentration of viruses in soil has been estimated to be $\sim 10^9$ virus particles g^{-1} dry weight (Williamson et al. 2005; Swanson et al. 2009). A lower estimate of the concentration of viruses in soils of $\sim 1.5 \times 10^8 \text{ g}^{-1}$ (Ashelford et al. 2003) can be explained at least in part by being based on wet weight figures as the water content of the soil is $\sim 56\%$. These figures are much higher than the concentrations reported of viruses in marine environments of $\sim 10^6\text{--}10^8$ virus particles ml^{-1} (Guixa-Boixereu et al. 2002; Ortmann and Suttle 2005). It has been estimated, based on the abundance of viruses in marine environments, that they contain ~ 200 Mt of carbon and are the second largest component of biomass after prokaryotes (Suttle 2005). The corresponding figures for viruses in soils are likely to be many times greater given that more than 90 % of the world's bacterial population and most of its diversity is contained in soils (Curtis et al. 2002). Despite this, viruses in soils have been the focus of relatively few studies due at least in part to technical difficulties which have only recently been at least partially overcome.

The latest report of the International Committee on Taxonomy of Viruses recognises approximately 2,300 viruses (King et al. 2011). It has become clear in the last decade that virus particles are abundant in the wider environment (Suttle 2005, 2007; Ashelford et al. 2003; Williamson et al. 2005, 2007b; Brussow and Kutter 2005) and metagenomic analyses have revealed novel virus assemblages that exist in the environment (Dinsdale et al. 2008; Breitbart and Rohwer 2005; Fierer et al. 2007; Breitbart et al. 2002, 2004a) indicating that the known viruses are a gross underestimate of the extent of virus diversity. It has also become clear that the known viruses are not necessarily representative of the total virus populations in the wider environment (Kristensen et al. 2009).

Most of the studies of virus populations in the wider environment have been performed using samples of marine or aquatic environments. Relatively little is known about viruses in soils and their ecological significance, and it is only in the last 10 years that even basic information such as virus abundance in soils has been measured. Therefore questions of how supportive viruses in soil can be for soil microbial functioning and for plant health, or what deleterious effects they may have are open ones which require further work to characterise more fully the diversity of viruses in soils, and their potential interactions with microbial communities and higher organisms. This chapter will review the information that is known about virus abundance and diversity in soils, taking a broad view that includes not only free virus particles in soils but also viruses that can exist within soil-inhabiting organisms such as vector-transmitted plant pathogenic viruses, and viruses that incorporate their genomes into that of their host microorganisms. It will discuss how the presence of plant pathogenic viruses in soil can infect plants and directly cause negative effects in the plant. Viruses infecting micro-organisms in the soil may possibly influence microbial communities in soils with positive or negative effects to plants. Analogies with information derived from studies of marine viruses will be

explored and we will highlight where these analogies may be weak. Finally there will be a discussion of the areas of research that need to be addressed to begin to provide a greater understanding of the ecological and evolutionary functioning of viruses within soils.

8.2 Abundance and Diversity of Viruses in Soils

The first direct measurements of the abundance of viruses in soils were performed by transmission electron microscopy (TEM) and looked at viruses present in rhizosphere soil (Ashelford et al. 2003). This showed the presence of both tailed bacteriophages and other virus particles which were present with a total abundance of $\sim 1.5 \times 10^8 \text{ g}^{-1}$ which was equivalent to 4 % of the bacterial population ($3.6 \times 10^9 \text{ g}^{-1}$). Much higher ratios of virus to bacteria were observed in a study of different soil types in Delaware, USA, and ranged from 10 to 3,000 virus: bacteria depending on the soil type (Williamson et al. 2005). The majority of the soil viruses were tailed bacteriophages of the order *Caudovirales*, which could be expected, as tailed bacteriophages of this order account for 95 % of all known bacteriophages (McGrath and van Sinderen 2007). Land use practices appear to have a significant effect on both bacterial and virus populations. Virus abundance was directly correlated with soil water content and viruses were most abundant in wetland forest soil samples but much lower virus abundance was observed in drier, agricultural soils. Virus morphological diversity was also greater in forested than agricultural soil. However, the ratio of virus to bacteria was much higher in the drier agricultural soils than in forested soils even though the abundance of both viruses and bacteria was much lower in the agricultural soils (Williamson et al. 2005).

Swanson et al. (2009) found a greater diversity of virus morphologies in soil samples from Scotland using a more stringent purification technique. The numbers of tailed bacteriophages ($\sim 4.8 \times 10^7/\text{g}$ dry weight) were similar to previous reports but only comprised ~ 4 % of the total virus particles in the Scottish soil whereas tailed bacteriophages predominated in other soils examined (Ackermann 2007; Williamson et al. 2005). In addition, the Scottish soil contained small spherical virus particles similar in size to single-stranded (ss)RNA containing bacteriophages of the *Leviviridae* family or to some plant viruses, and larger spherical viruses similar to the double-stranded (ds)DNA containing viruses of the *Partitiviridae*, *Chrysoviridae* and *Totiviridae* families. Bacilliform particles similar to the ssRNA containing *Barnaviridae* family, rod-shaped particles similar to the ssDNA containing *Inoviridae* family and filamentous virus particles were also present in the Scottish soil samples. Figure 8.1 shows some of the variety of virus types that have been found in soils. Virus abundance in the Scottish bulk soil was similar to that found in rhizosphere or rhizosheath samples. This results in a higher virus-to-bacteria ratio being measured in bulk soil (4.68) compared to that in rhizosphere or rhizosheath (0.27) samples due to the lower numbers of bacteria in the bulk soil when compared to the rhizosphere or rhizosheath samples (Swanson et al. 2009).

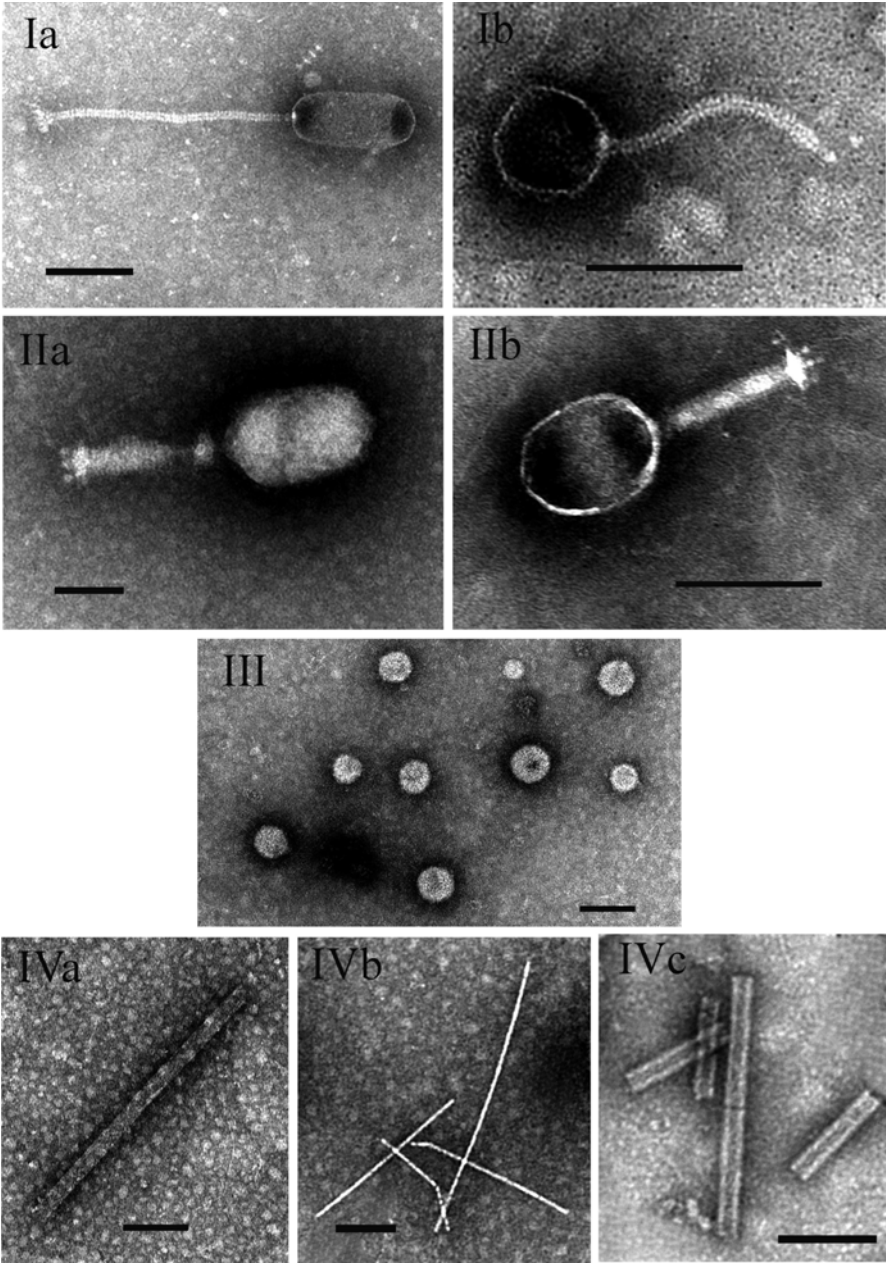


Fig. 8.1 Transmission electron microscopy images of virus particles isolated from soil. (**Ia** and **Ib**) Siphovirus particles. (**IIa** and **IIb**) Myovirus particles. (**III**) spherical virus particles of different sizes. (**IVa**) Thick filamentous particle. (**IVb**) Thin filamentous particles. (**IVc**) rod-shaped particles. Bars=100 nm

Bacteriophages have also been recovered from surface sands of the Sahara desert, but only after induction of their release from bacterial cells by mitomycin C, a potent DNA crosslinking compound that causes cell death (Prigent et al. 2005). In addition to existing as free individual phage particles can also exist as prophages (virus DNA integrated into the bacterial genome or existing extrachromasomally as plasmids) or as particles within the cytoplasm of bacteria. Mitomycin C can induce the release of these other forms of some bacteriophages and result in lytic infection and release of virus particles. Diverse viruses of the *Myoviridae*, *Siphoviridae* and *Podoviridae* families with genomes ranging in size from 45 to 270 kb were found in the Sahara desert surface sands after this treatment and a purification procedure that enriched for bacteriophages with dsDNA genomes. Twenty different morphologies and sizes of bacteriophages belonging to the *Myoviridae* and *Siphoviridae* families have also been isolated from surface sands from the Namib Desert using similar Mitomycin C induction methods. In this case the size of the genomes of most of these viruses was 55–65 kb with some genomes being as large as 350 kb (Prestel et al. 2008). Presumably, the harsh conditions of desiccation and ultra-violet-irradiation from the sun in desert surface sands reduces the numbers of free virus particles to below a detectable level by microscopy, and this is why detectable numbers of virus particles are only observed after mitomycin C induction of the host bacteria. Epifluorescence techniques were used to detect viruses in topsoil of a number of samples from desert dust storm regions and virus: bacteria ratios in these ranged from 0.15 to 1.66 (Gonzalez-Martin et al. 2012).

Some caution should be exercised in coming to comparative conclusions between the studies described above as differences in the extraction and visualisation methods used can affect the observed trends in virus abundance (Williamson et al. 2013). Also tail loss from bacteriophage particles during extraction from soil occurs more frequently among members of the *Siphoviridae* family than with other tailed bacteriophages and this can result in a bias during observations of relative virus occurrence made using TEM (Williamson et al. 2012). Thus it is difficult to make meaningful comparisons between the different reports of virus diversity and abundance in soils.

An alternative approach to the visualisation methods used above to study the presence of viruses in soils is metagenomic sequencing studies which seek to determine genetic sequences from all the virus genomes (sometimes referred to as the virome) present within an environmental sample. Sequence analysis of randomly chosen cDNA clones from viral metagenomic libraries showed that similar types of bacteriophages are found in prairie, desert and rainforest soils (Fierer et al. 2007). The majority of these bacteriophage sequences showed no significant similarity to previously described virus sequences, and the majority of 4,577 virus-related nucleotide sequences derived from soils in different ecosystems had no similarity to sequences reported in databases. The richness of viruses in all three soil types exceeded that of bacteria with the highest being in rainforest soils where the virus richness was an order of magnitude greater than that of bacteria. It also appears that soil viruses, bacteria, Archaea and fungi are globally diverse with little phylogenetic overlap being found between soil samples. In fact only one overlapping

bacteriophage sequence out of 4,577 sequences was identified in the samples examined. It would seem that the diversity of virus genotypes within soils is up to 1,000 fold higher than that found in aquatic environments (Breitbart et al. 2004a; Fierer et al. 2007). However, at least some viruses are able to move between environments and sequences from a T7-like bacteriophage have been shown to have a global distribution in different ecosystems (Breitbart et al. 2004b). A modified cloning and sequencing approach revealed the presence of ssDNA viruses in rice paddy field soil as well as the dsDNA bacteriophages of the *Siphoviridae*, *Myoviridae*, *Podoviridae* and *Tectiviridae* families that were found in other soils. The ssDNA-containing viruses were identified as members of the *Microviridae* family which infect bacteria, and of the *Circoviridae*, *Nanoviridae* and *Geminiviridae* families which infect eukaryotes (either plants or animals). The eukaryotic virus sequences comprised 85 % of the ssDNA virus sequences and the ssDNA bacteriophage sequences were 15 % of this total. The eukaryotic viruses probably originated from the rice plants or other plants, and from animal faeces and manure (Kim et al. 2008).

Soils clearly act as reservoirs of viruses but these are probably not entirely static reservoirs as at least some viruses seem to move readily between environments (Breitbart and Rohwer 2005). One bacteriophage-encoded DNA polymerase sequence (HECTOR), for example, was found in marine and saltern waters, associated with corals, in rumen fluid and in soil (Breitbart et al. 2004a, b). The observation of DNA sequences from a bacteriophage (MZTP02) that was first isolated in China within the genomes of two different bacteriophages isolated from an Antarctic soil sample also indicates that some bacteriophages may move readily between geographic locations (Swanson et al. 2012). Alternatively, some bacteriophages may be ubiquitous as is the case with some bacteriophages which have been reported to have a global distribution (Breitbart and Rohwer 2005; Breitbart et al. 2004b; Thurber 2009). In addition to the bacteriophages described above it is important to remember that soils can contain viruses that infect plants and that these can have direct pathogenic effects in plants. Also viruses such Hepatitis A virus, poliovirus and other enteric viruses that are pathogenic to humans and animals have also been detected in soils (Santamaria and Toranzos 2003). These viruses presumably originate in waste water or as organic wastes used as fertilisers.

8.3 Effects of Viruses Pathogenic to Soil-Inhabiting Organisms

One way that viruses in soils could have potential benefits for plants is by infecting organisms that are pathogenic for plants. Examples of these would be viruses of oomycetes such as *Phytophthora* spp. (Cai and Hillman 2013). Viruses also infect filamentous fungi and may have some potential as biocontrol agents with, in some cases, relatively wide host range (Pearson et al. 2009; Lee et al. 2011). The first report of viruses in nematodes was of two viruses from *Caenorhabditis elegans* and *C. briggsae* that bore similarities to the positive –stranded RNA viruses of the

Nodavirus family (Felix et al. 2011). Subsequently four distinct viruses with negative-stranded RNA genomes were isolated from the plant pathogenic nematode, soybean cyst nematode, demonstrating the potential diversity of viruses that can infect nematodes (Bekal et al. 2011).

As already stated, relatively little is known about viruses that infect bacteria in soils and it is difficult to determine accurately the effects that viruses may have on soil microbial communities. A reduction in bacteriophage abundance in an arctic soil system was caused by addition of an anti-viral agent and resulted in increases in both microbial biomass and respiration indicating that virus infection has a regulatory role in microbial activity (Allen et al. 2010). We can also look at the situation in marine environments and expect that the situation in soils may be analogous. Estimates of mortality for bacteria in marine environments range from 4 to 50 % of bacteria produced every day being killed by bacteriophages (Heldal and Bratbak 1991; Steward et al. 1992). The frequency of infected bacteria appears to increase with bacterial abundance in marine environments and viruses may play a more important role in controlling bacteria at high densities, with predatory grazing of bacteria being more important at lower bacterial densities (Weinbauer and Peduzzi 1995). Viral lysis is more important than protozoan grazing in affecting microbial community composition in the bathypelagic zone of the north-western Mediterranean and there seems to be a strong codevelopment of virus and host communities in these deep waters (Winter and Weinbauer 2010). Virus-induced mortality of prokaryotes appears to increase with water depth in marine sediments with mortality rates ranging from ~16 % in coastal sediments to ~89 % in sediments beneath 1,000 m depth (Danovaro et al. 2008). In this study >99 % of infections resulted in lysis of the host cell indicating that viruses are the major cause of prokaryotic mortality in deep sea sediments. Metagenomic analysis of a near-shore marine sediment indicated that 79 % of the bacteriophage present were either prophage or Siphophage (Breitbart et al. 2004a). Siphoviruses are temperate bacteriophage that can persist with their genomes integrated into the DNA of their host in a process known as lysogeny and prophages are derived from this integrated state (see discussion of gene transfer below). Consequently, the host cell does not lyse while the bacteriophage genome remains integrated. This occurrence of temperate bacteriophage compares with less than 50 % of Siphoviruses and prophage in water column samples (Breitbart et al. 2002) and suggests that conditions favouring lytic infections are more prevalent in the water column and with increasing depth of marine sediments. Some studies have failed to show a significant effect of viruses on bacterial mortality and it may be that the effect of viruses is sporadic, both temporally and geographically (Fuhrman 1999).

Viruses can cause significant effects on the relative proportions of different species and strains within an environment. Viruses in marine environments and in soils would be expected to be spread by passive diffusion. Consequently, more abundant hosts would be expected to be more susceptible to virus infection as the probability of a virus reaching a susceptible host within the time it remains infectious would be greater than for a less abundant host. Bacteriophages and presumably their hosts, are locally adapted in soils with bacteriophages being more able to infect bacteria from the site from which they were sampled than bacteria from other sites even just

a few centimetres away (Vos et al. 2009). This high degree of local adaptation occurs despite the fact that the site sampled was a grazed flood plain, both of which are factors which would be expected to increase homogenisation over such small spatial scales. Rapid coevolution between bacteria and bacteriophages has been demonstrated in soil in a manner that is consistent with virus genotypes specialising on host genotypes, with the fitness of any given genotype fluctuating through time (Gómez and Buckling 2011). Fluctuating selection dynamics is important as it has the potential to continue indefinitely and can maintain genetic diversity within a community. Modelling has shown that virus infection in communities can act to prevent any single fast-growing microbe from dominating an environment through a “Kill the Winner” mechanism in the competition for nutrients thus maintaining a dynamic equilibrium within the community (Thingstad 2000; Thingstad and Lignell 1997; Winter et al. 2010). Microcosm experiments have shown that soil virus assemblages respond rapidly to changes in host growth and can also be rapidly lost from a system instead of the situation being a slow and unchanging process (Srinivasiah et al. 2008). Also, viral lysis of microbes may not necessarily be entirely detrimental as viral lysates can act as sources of organic and inorganic nutrients for other microbes. Virus-induced mortality of prokaryotes in deep-sea sediments can reduce competition for resources while simultaneously generating nutrients for uninfected prokaryotes (Danovaro et al. 2008). In a model system, viral lysis of the autotrophic flagellate *Phaeocystis pouchetii* stimulated other microbial growth by a transfer of organic material from the *P. pouchetii* lysates, and also led to regeneration of N and P by mineralisation (Haaber and Middelboe 2009). This supports the hypothesis that viral lysates can be a source of inorganic nutrients, at least in marine systems. Viruses may therefore have an important role in directing nutrients back towards other microbial organisms instead of into food chains as would happen as a result of predatory grazing of bacteria by other organisms.

Bacteriophages have been shown to have a potentially deleterious effect on growth of sugar beets by infecting fluorescent *Pseudomonas* spp. and preventing their colonisation of the plant roots (Suslow and Schroth 1982; Stephens et al. 1987). A lytic bacteriophage, ΦGP100, that reduced the population size of the beneficial *P. fluorescens* CHA0 strain by 100-fold in soil and on cucumber roots has been identified. This resulted in a loss of the biocontrol capacity of the *P. fluorescens* CHA0 against infection of cucumber plants by *Pythium ultimum* and severely reduced growth and survival of the cucumber plants. The protective effect was restored by a spontaneous ΦGP100-resistant variant of *P. fluorescens* CHA0 and the use of such resistant variants may improve the persistence and beneficial effects of bacterial inoculants in soils (Keel et al. 2002). Bacteriophages have also been shown to have an effect on rhizobial bacterial strains. In glasshouse experiments a bacteriophage specific for *Bradyrhizobium japonicum* USDA 117 reduced the population of the bacteria in soil and this resulted in decreases in the nodule number, nodule fresh weight, plant dry weight and nitrogenase activity on soybean (*Glycine max*) (Hashem and Angle 1988). This bacteriophage also had similar effects in field conditions, and significant reductions in nodule weight and number, shoot weight, nitrogenase activity and seed index were observed when soybean was grown in soil

inoculated with *B. japonicum* USDA 117 along with this bacteriophage when compared to plants grown in soil inoculated with *B. japonicum* USDA 117 alone. In competition experiments a bacteriophage-resistant *B. japonicum* strain (USDA 110) was able to colonise nodules more effectively when *B. japonicum* USDA 117 was present with the bacteriophage than when in direct competition with *B. japonicum* USDA 117 alone. This raises the possibility that nodulation by selective strains of rhizobia could be manipulated by addition of appropriate bacteriophages (Hashem and Angle 1990).

It is possible for bacteria to develop resistance to infection by bacteriophages but this is likely to come at a cost to the bacteria. Recent studies with *Pseudomonas aeruginosa* and two bacteriophages, either separately or in combination, showed that development of resistance can result in lower growth rates, less biofilm production, decreased motility and changes to virulence determinants. The precise cost of resistance depends on the host-bacteriophage system involved and changes persisted after the bacteriophage selection was removed (Hosseinioust et al. 2013).

8.4 Plant-Pathogenic Viruses in Soil

There are three ways in which plants can potentially be infected by pathogenic viruses in soils: mechanical, by nematode vectors or by fungal vectors.

The main ways in which plant viruses infect plants are following transmission by invertebrate vectors, by vegetative means, or through seed or pollen. Infection of plants by freely-existing virus particles in soils is of relatively minor importance. Soil that contains debris from previously infected plants can act as an inoculum source for infection of plants via wounds on the plant surface and Tobacco mosaic virus (TMV) can be inoculated onto leaves of plants in this way. TMV and a small number of other plant viruses appear to infect roots of plants without any vector being involved. Some freely existing plant viruses including TMV can also be transmitted to plants from soil on contaminated machinery or farm implements, and by movement by animals or humans (Hull 2002).

Some plant pathogenic viruses can be transmitted by ectoparasitic, soil-inhabiting nematodes belonging to the *Longidoridae* and *Trichodoridae* families of the *Dorylaimida* or *Triplonchida* orders respectively (for review see Brown et al. 1995). Economically important examples of such viruses are raspberry ringspot virus and tobacco rattle virus. Two genera of plant viruses can be transmitted by these nematodes. Nepoviruses are transmitted by species in the *Xiphinema* and *Longidorus* genera of the *Longidoridae*, and tobraviruses are transmitted by species in the *Trichodorus* and *Paratrichodorus* genera of the *Trichodoridae*. There is significant, but not total, specificity in transmission of viruses by nematodes and the virus coat protein is the sole determinant of specificity for nepoviruses. The situation is slightly different for tobraviruses with a second gene, 2b, being important for transmission in addition to the coat protein (MacFarlane 2003). Both nepoviruses and tobraviruses can persist in a non-replicative manner in nematodes for months or years after

a nematode, either juvenile or adult, has fed on the roots of an infected plant depending on the virus and nematode combination. Infection of subsequent plants occurs when a viruliferous nematode feeds on uninfected plants. Nematodes lose their virus after moulting between each of the four stages of juvenile development.

Other groups of plant viruses can be transmitted by soil-inhabiting fungi which are obligate parasites of plant roots, specifically two species of Chytridiomycetes: *Olpidium brassicae* and *O. bornovanus*, and three species of Plasmodiophoromycetes: *Polymyxa graminis*, *P. betae* and *Spongospora subterranea* (for review see Campbell 1996). Examples of these viruses are soil borne wheat mosaic virus, tobacco necrosis virus and potato mop-top virus. Various degrees of host specificity exist among these fungal vectors with some being highly specific in which plants they infect while others have quite a broad host range. The Chytridiomycete fungal hosts transmit isometric viruses which are taken up by zoospores from soil water. The Plasmodiophoromycete hosts on the other hand transmit rod-shaped or filamentous viruses which are acquired by zoospores when they are within the root of an infected plant. Irrespective of the method of acquisition, viruses can survive for many years in vegetative sporangia, or resting spores that are formed as part of the life cycle of these fungi. These resting spores can persist in soil between crops until as yet unidentified environmental signals induce them to produce zoospores that initiate another round of infection. Movement of contaminated soil on farm machinery or clothing or attached to plant material is an important method of transmission for both fungus- and nematode-transmitted viruses.

Most of the plant-pathogenic soil-borne viruses that have been identified so far infect economically-important plants. However, there is no reason to expect that such transmission does not necessarily occur to other uncultivated plant species. Control of nematode- and fungus-transmitted plant-pathogenic viruses by chemical treatment of seeds and soil, or by soil fumigation is largely not possible at least in Europe due to adverse effects and toxicity of the chemicals whose use has now been largely banned. Attempts to breed plants resistant to some of these viruses have met with mixed results (Kühne 2009; Santala et al. 2010). Transgenic approaches to resistance to some of these viruses have shown some promise but face regulatory constraints and problems with public acceptance of the technology (Reavy et al. 1995; Barker et al. 1998; Vassilakos et al. 2008).

8.5 Gene Transfer

The main way in which viruses in soils could act in a beneficial manner is by transferring genes between microbial hosts by horizontal gene transfer that can be mediated by a process known as transduction or lysogenic conversion (Brussow et al. 2004). In lysogeny a bacteriophage genome can become integrated into the host bacterial cell chromosome where it can remain in a stable state known as a prophage. Subsequent excision of the prophage from the bacterial chromosome can be inexact and DNA from the host chromosome can be packaged as part of the

bacteriophage genome into virus particles known as transducing bacteriophages. The host gene can then be transferred to a new host following infection of a bacterial cell by the transducing bacteriophage (Paul and Jiang 2001). A particular class of transferred genes, known as ‘morons’ have been identified as protein-coding sequences flanked by transcription initiation and termination sequences and situated between two bacteriophage genes in a bacteriophage genomes. Morons seem to have entered phage genomes comparatively recently and may be expressed from the repressed prophage when integrated into the bacterial genome (Juhala et al. 2000). Phylogenetic analysis of proteins involved in nucleic acid metabolism has shown that gene transfer events between cells and viruses are numerous and suggests that viruses have played a major role in the evolution of cellular genomes (Filée et al. 2003).

Lysogeny among soil bacteria is common and occurs with a frequency of 4–66 % depending on the soil type with Antarctic soil having a frequency of 4.6–21 % and Delaware, U.S. soils having a frequency of 22.1–66.7 % (Williamson et al. 2007a, 2008). Lysogeny frequencies as high as 85 % have been reported for soil bacteria (Ghosh et al. 2008) and it may be that lysogeny is particularly beneficial for soil bacteriophages due to the patchy distribution and low growth rates of their hosts in soil and that this favours lysogenic colonies that are able to better secure resources (Stewart and Levin 1984). This is in contrast to aquatic environments and deep-sea sediments where virulence seems to be more successful for phage populations (Marsh and Wellington 2006). Transducing bacteriophages, which transfer host genes, have long been known to be responsible for significant gene transfer between bacteria (Frost et al. 2005). The frequency of transduction in natural environments is likely to be significantly lower than the once in every 10^8 phage infections that can be observed in laboratory conditions. However, the large global population of bacteriophage ($>10^{30}$) means that the rate of bacteriophage-mediated gene transfer in bacteria is estimated to be $\sim 20 \times 10^{15}$ gene transfer events second^{-1} (Bushman 2002). The total amount of DNA transferred between bacteria by transducing bacteriophages is also estimated to be 10^{28} base pairs (bp) year^{-1} , possibly representing $\sim 10^{24}$ genes (Rohwer and Thurber 2009). An alternative way to consider these figures is that bacterial genomes vary in size from 5×10^6 – 10^7 bp (Casjens 1998) which means that transducing bacteriophages could be transferring the equivalent of the total genomes of $>10^{21}$ bacteria each year. An analysis of the occurrence of prophages integrated into bacterial genomes has produced estimates that they account for up to 20 % of some bacterial genomes, though some bacteria have been found to be completely free of prophages (Casjens 2003). The relatively high amount of lysogeny observed in soil bacteria will increase the genetic diversity of the soil microbial community. The exact extent to which this drives the functioning of soil microbial communities and consequent effects on plants is not entirely clear but is likely to be significant.

Gene Transfer Agents (GTAs) have also been identified as virus capsids that package random fragments of host bacterial genomes. GTA-like genes are present in most species of α -proteobacteria that have been sequenced indicating that they originated in a single GTA-containing ancestor (Lang and Beatty 2006). In marine environments GTAs have been shown to transfer genes between bacteria at a

frequency up to 31 million times greater than that of transduction by bacteriophages (McDaniel et al. 2010). Analysis of marine virus metagenomic data raises the possibility that GTAs are predominant in the virus samples (Kristensen et al. 2009). If this is the case, the transfer of genetic information between prokaryotes by virus like entities such as GTAs could be much more extensive than previously thought. Since most of the sequences identified in virus metagenomic analyses have no match to sequences in databases it may be that this extensive transfer of genetic information could be resulting in an increase in the transfer of comparatively rare genes (Kristensen et al. 2009).

The finding of the almost complete genome of the MZTP02 bacteriophage within the genomes of two bacteriophages isolated from the Antarctic has revealed a novel nested architecture of virus genome arrangement (Swanson et al. 2012). This indicates a previously unsuspected type of genetic recombination event occurring in virus evolution. The implications of this for production of novel bacteriophage genomes and gene transfer are currently unclear but it would appear that the process could have been responsible for allowing MZTP02 DNA sequences to enter *Staphylococcus pasteurii*, which it does not normally infect, from a *Bacillus* spp. The formation of hybrid genomes enabling a broadening of host range could confer an evolutionary advantage in environments such as the Antarctic where bacterial hosts are present in low density as indicated by small microbial biomass (Barrett et al. 2006; Hopkins et al. 2006a, b) and the large bacteriophage-to-bacteria ratio (Williamson et al. 2007a), or where the resource supply is sparse and intermittent (Hopkins et al. 2006a).

An examination of metagenomic sequence data from nine biomes showed that viromes carried the same diversity of genes involved in metabolic functions as is contained in the microbial communities isolated from the same environments. Furthermore, all the environments examined had the same diversity of genes, i.e. most of the genetic functional diversity was maintained in all environments (Dinsdale et al. 2008). However there was an enrichment of specific genes in different environments leading to low functional evenness in the viromes with the frequency of genes reflecting the importance of particular metabolic functions within an environment. The presence of 130 out of a possible 157 genes encoding motility and chemotaxis proteins in the viromes was unexpected as viruses are non-motile and this is a surprising example of a specialised metabolism being present in the viromes. The high taxonomic evenness observed in microbial and viral communities (Angly et al. 2006) led Dinsdale et al. (2008) to suggest that horizontal gene transfer has a major role, possibly even greater than taxonomic changes among microbial populations, in controlling gene distribution in an environment. Numerous genes encoding metabolic and cellular functions have also been identified in other marine viromes suggesting that virus communities act as reservoirs of important genetic material (Angly et al. 2006; Williamson et al. 2008). The genes encoded in bacteriophage genomes can even include ones involved in such fundamental processes as photosynthesis (Mann et al. 2003). A study of 33 marine cyanobacterial viruses found that 88 % contained photosynthesis genes (Sullivan et al. 2006). These genes appear to have been transferred in a number of discrete events and that the exchanges occurred from host to bacteriophage, bacteriophage to host and within the bacteriophage

gene pool itself. Gene exchange and genetic recombination arising from co-infections within the bacteriophage gene pool creates a reservoir of gene variants that can subsequently be acquired by the hosts. Therefore, the bacterial and bacteriophage gene pools can be regarded as overlapping with exchange between the pools resulting in evolutionary changes for both host and virus.

Few metagenomic studies have yet been carried out on viruses from soil. Our preliminary sequencing of randomly amplified DNA fragments from viruses isolated from a type of soil known as Machair soil from the north west of Scotland has identified the presence of genes related to those found in iron-oxidising and iron-reducing bacteria (Brian Reavy, unpublished). This could be significant as Machair soils are low in available iron content. This highlights the need for further detailed metagenomic studies of soil viromes to determine the genetic constituents and possible roles of the virus populations in soil microbial community functioning.

8.6 Future Prospects

Microbial organisms are vital for the functioning of soils in maintaining soil fertility and supporting plant growth. It is becoming increasingly clear that viruses of these microbes as pathogens have an important role in regulating the population structure of their microbial hosts. Virus populations may also act as reservoirs of genes involved in all the biochemical functioning of their microbial hosts, and by recombination among themselves during co-infections, could be a source of new gene variants. The extent to which both of these processes occur remains uncertain.

Some analogies have been drawn with virus populations in aquatic systems, where some key principles, such as the importance of viruses as reservoirs of genetic material and as drivers of genetic change in bacterial hosts, are probably true for both types of environment. It is important to note, however, that virus populations in soils may be structured and behave in quite different ways than those in aquatic systems. It is possible that soil virus assemblages are very different to aquatic ones (Srinivasiah et al. 2008) and that the diversity of soil virus genotypes is much greater than that found in aquatic environments (Breitbart et al. 2004a; Fierer et al. 2007). Also, virus populations in soils appear to have greater local adaptation than viruses in aquatic environments (Vos et al. 2009). The concentration of viruses in soils is probably an order of magnitude greater than that found in aquatic environments, on a volume basis, and the virus: bacteria ratio is also higher in soils than aquatic environments (Williamson et al. 2005; Swanson et al. 2009). It is also possible that production of viruses is slower in soils than in aquatic environments. Lysogeny may be more prevalent as a survival and reproductive strategy in soil environments than in aquatic environments (Marsh and Wellington 2006). All of these factors require study in greater detail to establish a more complete picture of the structure of soil virus populations. In addition, metagenomic analyses need to correlate the genetic constituents of soil viromes with the physio-chemical and biological characteristics of

the soil environments from which they are isolated to understand the functional roles more fully.

One important question that remains unanswered is to what extent the virome drives metabolic functioning in microbial communities or whether it simply reflects the broader microbial diversity. Genetic exchanges between viruses may give rise to new variants of host genes that could then be utilised by host cells. Genome sequencing and transcriptomic studies of host microbes will be required to determine the extent to which metabolically important genes are expressed from prophages. Another possible role for viruses could be to spread or amplify the presence of beneficial genes that arise within microbial communities in response to environmental changes. Further work is required to examine the extent of these and other possibilities and their importance to soil microbial communities. Related to environmental changes is the question of how virus populations and the relatively large percentage of lysogens in soils may react to such changes, and how they may affect microbial population structures and functioning.

The prevalence of the specialised Gene Transfer Agents among virus particle populations in the environment is presently unclear as is the full extent of their role in gene transfer and in driving evolution of their hosts' genomes. The question of whether they have a greater or lesser role than bacteriophages in this regard is also important to address. Gene Transfer Agents may facilitate transfer of host genes between bacteria but would not necessarily lead to the genetic variability that may arise as a result of recombination between bacteriophages.

Archaea form a distinct domain of life and contribute significantly to global nutrient cycling. They also have essential roles in ammonia oxidation where they outnumber bacterial ammonia oxidisers, and in methanogenesis during decomposition of organic material in anaerobic environments. Archaea are also distinct at a genetic level with large numbers of their genes having no homologues in other life forms (Jarrell et al. 2011). Viruses that infect Archaea are also novel both in structure and genetic composition with most of their genes having no known functions (Lawrence et al. 2009). The ecological and evolutionary roles of these viruses are unknown and are other areas of research that requires study.

Soil-borne plant pathogenic viruses may become an increasing economic problem in crop plants as the traditional chemical controls used for their nematode and fungal vectors is removed. Control of these infections will rely in the future more on genetic control either through host resistance genes or transgenic approaches. A greater understanding of virus-host interactions in these infections is required to facilitate this.

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Chapter 9

Soils Suppressing and Promoting Non-native Plant Invasions

Kenneth J. Elgersma

Abstract Non-native invasive plants are an increasing concern and are found on every continent on the globe, including Antarctica. While non-native invasives sometimes provide benefits to humans or wildlife, they often impair ecosystem services, crowding out native plant species, pre-empting scarce water and nutrients, and creating novel plant communities that can disrupt animal herbivore and pollinator communities. Many of these impacts have economic consequences for humans as well. Therefore, understanding and predicting invasions and their impacts has become a major challenge for ecologists. This chapter reviews ways in which soils influence the establishment and spread of non-native invasive plants. I focus first on the abiotic and biotic attributes, and their interactions, that influence the initial stage of invasion, which is heuristically defined as the stage before the non-native invasive has been present long enough or in densities high enough to substantially alter soil properties. Then I describe ways in which non-native invasive plants alter these soil properties and discuss potential feedback effects on invasion rate that result from these invasion-induced changes. I also suggest some areas where further research could be useful to improve our understanding of when and how soils suppress or promote non-native invasive plants.

9.1 Effects of Soils on Invasion Rates

Soils can influence invasibility primarily through two largely connected aspects of soil: soil fertility (or productivity) and interactions with soil biota. While these aspects of soil are inter-related, they tend to be addressed by two largely separate

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bodies of literature (but see Schnitzer et al. 2011). In this section, I will review advances in these two areas of research, as well as the connections that have been drawn between these two bodies of literature. I then suggest avenues of further research which could be useful ways to connect these two inter-dependent aspects.

9.1.1 Soil Fertility and the Productivity – Invasibility Relationship

Many early studies on plant invasions in the 1980s and 1990s noted that invasive species dominate in nutrient-rich soils, and Ehrenfeld (2003) formalized this observation in a meta-analysis. Because high-fertility soils, associated with high rates of nutrient cycling, have large supplies of nutrients available for plant growth, it would seem logical to hypothesize that higher nutrient availability provides greater opportunity for some of these resources to be preempted by invasive plants and allow invasive species to establish. This “empty niche” logic linking soil fertility and invasion was in fact touched on very early by Charles Elton (1958) in his seminal book on biological invasions. Elton’s book was strongly influenced by the prevailing niche-based ecology of the time, and to complete the logical argument, the “empty niche” theory had to explain why native species do not utilize the additional resources found in high-resource soils, or in other words, why do increased nutrient supply rates create open niches? Elton explained this by suggesting that anthropogenically “simplified” habitats with lower species diversity have more unused resources because there are fewer species taking up resources, creating empty niches that provide greater opportunity for invasion. Thus, high-nutrient soils were thought to support invasion indirectly because of anthropogenically-reduced species diversity.

This hypothesized relationship between invasibility and diversity (rather than soil fertility) garnered much of the subsequent attention in invasion biology, and a large and sometimes thorny body of research developed on the relationship between diversity and invasibility (reviewed in Fridley et al. 2007). One of the issues continually arising from this body of research, however, was that diversity is an emergent community-level property that is correlated with many known and unknown ecological drivers, including (but not limited to) soil fertility, disturbance, predation and herbivory, and even the identities of the native species in the community (Hierro et al. 2006; Sandel and Corbin 2010). Furthermore, many of these factors interact in shaping plant community structure (Mattingly et al. 2009). Knops et al. (1999) found little evidence, for example, that species diversity directly influences invasibility; rather high diversity reduced available light and nitrogen, which was correlated with the observed reduction in invasion rates. While this suggests low soil fertility suppresses invasion, Knops et al. (1999) also found that high diversity increased the density and diversity of insect herbivores and severity of disease outbreaks, both of which might have contributed to observed effects on invasion rates. Thus, early experimental work demonstrated the complexity of interactions that can modulate the effects of soil fertility on invasibility.

This finding was further emphasized by observational studies that revealed much more variable diversity-invasibility patterns and sometimes showed results opposite to those found in experimental studies, especially when observations were done on large spatial scales (Fridley et al. 2007). These studies showed that sites with high native species richness, which typically also had high soil fertility, tended to also contain a high species richness of invasive plants. While this sparked strong debate about whether species richness of native and invasive species were positively or negatively correlated, the results are consistent with small-scale experimental studies in suggesting that fertile soils are supportive for exotic invasions, while low-fertility soils suppress invasive species, although the relationship is an indirect one mediated through species diversity.

Tests of the direct effect of fertility on invasibility generally support the hypothesis that fertile soils support greater invasion rates (Bradley et al. 2010). Greenhouse mesocosm studies which add nutrients to plant communities generally show invasives have a stronger competitive response to nutrients and a subsequently greater competitive effect on the native community (e.g., Green and Galatowitsch 2002). Similarly, adding high C:N amendments like sawdust or glucose to soils, which reduce available nitrogen through microbial immobilization, also often reduces the competitive success of invasives (Blumenthal et al. 2003; Perry et al. 2004), and this is presumably due to a direct effect of soil resource availability on invasibility.

While both large-scale and small-scale studies suggest fertile soils support greater exotic invasion, the debate sparked by the opposing relationships between native and exotic species richness in these different types of studies did bring to light caveats that are important to consider before drawing conclusions about the direct effects of soil fertility on invasibility. Much of the diversity debate focused on the mechanisms that might operate at large spatial scales but not in smaller experimental studies, some of which are relevant to relationship between fertility and invasibility. For example, soil fertility modulates the ecological effects of disturbance on plant community structure, so that the relationships between soil fertility, diversity, and invasibility depend on the disturbance regime (Hiero et al. 2006; Huston 2004). In low-fertility environments where plants are often slow to grow and reproduce, even relatively small disturbances can eliminate particularly slow-growing species with low reproductive rates. As a result, disturbance reduces species richness in low-fertility environments. However, disturbances can increase species richness in highly fertile environments by reducing the dominance of strong competitors (Huston 2004, but see Fox 2013). Using aquatic microcosms, Sperfeld et al. (2010) demonstrated that the positive productivity-invasibility correlation was due to an indirect effect of productivity through herbivory, rather than any direct effect supporting or suppressing invasion. These findings again underline the strong potential for indirect effects of soil fertility on invasibility, and caution against interpreting a positive relationship as evidence for increased empty niches.

Davis et al. (2000) formulated a slightly different and complementary niche-based argument relating soil fertility to invasibility. Their theory was simply that “a plant community becomes more susceptible to invasion whenever there is an increase in

the amount of unused resources” (Davis et al. 2000). While this theory is at its core very similar to the theory put forward by Elton 40 years prior, they elaborate on the mechanism by arguing that in addition to long-term average (equilibrium) resource levels, unused resources arise through short-term fluctuations either in resource supply or demand (Li and Stevens 2012). These fluctuating resources provide opportunities for both exotic and native species (Shea and Chesson 2002). This non-equilibrium niche theory therefore includes temporally-variable processes like herbivory and disturbance. Davies et al. (2005) expanded the theory further, showing spatial variability in resource supply or demand can also affect invasibility. Since spatial heterogeneity in resource supply often increases as mean resource levels increase (e.g., Gilliam et al. 2005), spatial heterogeneity could also contribute to the observed increase in invasibility in high-resource areas.

Finally, the debate over the relationship between native and exotic species richness also led to the observation that these relationships may not be arising from niche-based mechanisms at all. The viewpoint that invasion is driven by lack of competition for resources was firmly linked with the paradigm that plant communities are structured primarily by competition, a paradigm that has periodically been challenged, most recently and strongly in the early 2000s with Hubbel’s neutral theory (Hubbel 2001). The importance of neutral processes for exotic invasions is actively debated, but several studies have shown they may play an important role in shaping observations about invasibility. For example, positive native-exotic relationships at large spatial scales and negative relationship at small scales can arise through purely neutral processes (Fridley et al. 2004; Herben et al. 2004). This suggests that the observed relationship between native and exotic species richness may arise independent of soil fertility. Positive species interactions (i.e., facilitation) have also been largely underappreciated in ecology and may play an important role in the relationship between soil fertility and invasibility (von Holle 2013). A better understanding of the roles of neutral and positive species interactions in shaping plant community structure will help future development of theory and empirical tests of how soil fertility directly and indirectly suppresses or supports exotic invasive species.

To understand how soil fertility affects exotic invasion, there is also a need for a better understanding of the relationship between exotic species richness and exotic species dominance. Research on the relationship between native and invasive species diversity and between soil fertility and exotic species richness has focused primarily on species richness, with the implicit assumption that higher exotic richness is related to higher exotic dominance. Since dominance is the more relevant factor when considering the extent to which soils suppress or enhance invasive species’ growth either at the individual or population level, this is an important assumption. However, it is not clear that the assumption is supported; exotic species richness could conceivably increase independently of exotic species dominance.

Despite uncertainties about how fertile soils promote exotic invasion, restoration ecologists who are interested in creating invasion-resistant landscapes have begun experimenting with ways to reduce nutrient availability and create soils supportive of native plant growth. Non-agricultural ecosystems are globally receiving vastly

increased supplies of nitrogen (Reay et al. 2008), which is often a limiting or co-limiting resource for terrestrial plants (LeBauer and Treseder 2008). Increasing nitrogen deposition rates are widely viewed as a management concern due to effects on plant community invasibility, as well as strong negative effects on species diversity (Bobbink et al. 2010). As a result, there is wide research interest in reducing soil N availability using soil amendments, although there are significant logistical barriers to using this strategy on a large enough scale for management or restoration purposes (Vasquez et al. 2008).

Many of the studies that used C additions to reduce N availability and invasibility showed some degree of success, resulting in soils with temporarily lower available N that suppressed exotic invasive plant growth (reviewed in Alpert 2010). However, results have been mixed. Many studies showed suppression of native plant growth as well as exotic plant growth, and while exotics are often suppressed more than the natives, this is not always true (Alpert 2010; Sandel et al. 2011; Steers et al. 2011). The mixed success in suppressing invasions is at least in part because native and exotic species do not always differ very strongly in their relevant (nitrogen-use related) functional traits (Sandel et al. 2011; Steers et al. 2011). Several other limitations may further contribute to mixed success observed as well. The effects of C additions on soil nitrogen cycling are short-lived, typically disappearing after a couple months (Alpert 2010). Surface applications of C additions also change the physical properties of the soil-air interface, thereby changing rainfall interception and evaporation rates. Changes in soil moisture that result from surface applications can strongly affect plant competition (Dessserud and Naeth 2013), especially in arid or semi-arid grasslands.

Much of this work has been done in arid and semi-arid grasslands and shrublands, where implementing these treatments is logistically simpler. On one hand, this is logical because carbon additions are only likely to be logistically feasible in open habitats like grasslands. On the other hand, plants in these habitats tend to be either co-limited by water or even primarily limited by water, rather than by nitrogen. This suggests that C addition might be more effective at suppressing exotic invasives in mesic habitats such as wetlands or forests. Whether or not these results will translate into useful predictions for mesic habitats where N is more strongly limiting (e.g., forests, wetlands) is largely unknown and empirical tests are limited. In mesic grasslands, the few carbon addition studies to date were fairly successful in suppressing exotic plant cover and promoting native species replacement (Blumenthal et al. 2003; Prober et al. 2005). Carbon additions are seldom attempted in forests for logistical reasons, but Ross et al. (2011) found that two forest understory invaders were much more plastic in their responses to N availability than common native species, which explained why woodchips were ineffective in suppressing invasives (Ross 2008). Working in wetlands, Iannone and Galatowitsch (2008) added sawdust to plots and observed a short-term decline in soil inorganic N. This reduction suppressed invasion by *Phalaris arundinaceae* in the short term and shifted dominance toward native species, which were stronger competitors under low-N conditions (Perry et al. 2004). However, sawdust addition also caused a long-term increase in soil inorganic N as the sawdust gradually decomposed. This increased N could reverse

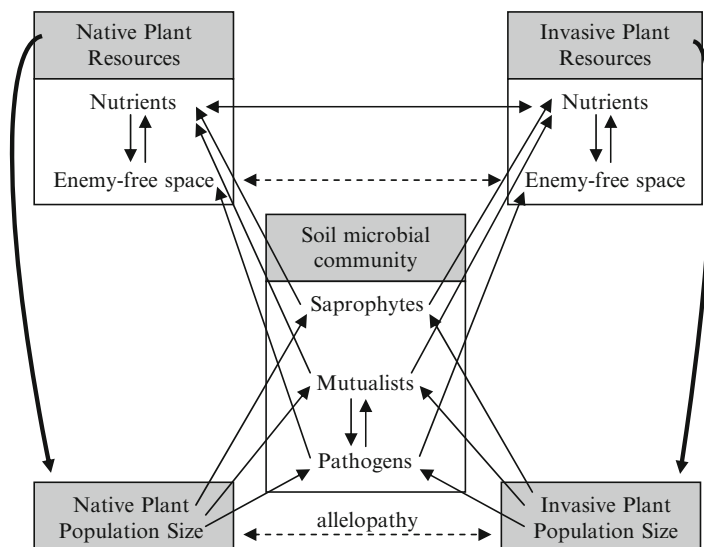


Fig. 9.1 Conceptual diagram of the belowground interactions that suppress or promote non-native invasive plant populations. *Arrows* indicate the direction of influence. Native and non-native plant populations influence interacting components of the soil microbial community, which influence the nutrients and enemy-free space available to native and non-native plant populations. Native and non-native plants also directly interact through allelopathy and root signaling

the suppression of *Phalaris* over the long term and lead to greater dominance of the exotic invader.

Carbon amendments reduce available N in the short term, but as the above example demonstrates, it can actually increase total ecosystem N by sequestering N in microbial biomass. If subsequent reductions in C availability, changes in soil moisture or temperature, or any number of other disturbances cause substantial mortality in the soil microbial community, sequestered N could be released as a nitrogen pulse, potentially resulting in greater invasibility (Davis et al. 2000). Thus, C amendments which are added to create soils that suppress exotic invasions in the short term might lead to soils which support exotic invasions in the long term. This concern could be reduced by combining C amendments with biomass removals (Perry et al. 2004) or burning to volatilize and remove N (Qian et al. 2009), though fire can also have a strong direct effect on exotic invasive plants (Keeley 2006) and the amount of volatilization depends on a complex suite of factors including combustion temperature and fuel load (Qian et al. 2009) (Fig. 9.1).

9.1.2 Soil Biota and Biotic Resistance to Invasion

The concept of an ecosystem or community resisting plant invasion dates back at least to Elton's seminal book, in which he discusses the "invasions which never happened" as encountering "resistance, whether by man or by nature or by man

mobilizing nature in his support” (Elton 1958, pp. 109–110). This concept, now often called “biotic resistance,” is important to understanding why soils suppress or support exotic invasive species. Biotic resistance to an exotic invader from soil biota results in soils that suppress the exotic, while lack of resistance or greater biotic resistance to native competitors promotes invasion (Bever 1994; Bever et al. 1997). The literature initially focused primarily on aboveground processes contributing to biotic resistance, but gradually incorporated belowground processes as well. The incorporation of belowground processes developed out of the confluence of research on Janzen-Connell hypothesis that density-dependent mortality contributes to the maintenance of diversity (Augsburger 1984; Mangan et al. 2010), with a rising interest in the influence of pathogens on community structure (Van der Putten and Peters 1997).

Much of this literature deals with plant-soil feedbacks, a topic that I discuss separately at the end of this chapter. In this section, I limit the discussion specifically to the biotic properties of soils which contribute to biotic resistance or lack of biotic resistance to invasion. In other words, I explore here the question of whether soil biota encountered during the initial stages of a new species’ introduction can influence the success or failure of that introduction. The degree of biotic resistance encountered by natives and exotic invasives in already-invaded soils, the resulting potential feedbacks, and repercussions for the invasion process are topics reserved for the conclusion of this chapter.

Although it is clear that the soil biota plays an important role in exotic plant invasion (Rout and Callaway 2012), relatively little is known about how soil biota affects the success during the initial stages of exotic introduction, perhaps because these initial stages of naturalization and invasion often go unnoticed and are understudied (Richardson and Pyšek 2012) or because the role of soil biota has frequently been overlooked in plant ecology (Bever et al. 2010). However, evidence indicates that besides the obvious requirements for appropriate climatic and environmental conditions (Richardson and Pyšek 2012), biotic factors, including soil biota, can play an important role in suppressing or supporting initial establishment of exotic plants (Mitchell et al. 2006).

Perhaps one of the clearest examples of soil biota suppressing invasion is the slow initial rate of invasion of invasive pine (*Pinus*) species in the southern hemisphere (Richardson et al. 2000). Pines are reliant on ectomycorrhizae (EM), and because other EM plants are relatively uncommon in areas in the southern hemisphere (e.g., southern Africa), these pine species’ ectomycorrhizal symbionts were largely lacking in these areas. As a result, many areas showed little or no invasion by pines. However, because pines are economically important timber species, EM-infected plants have been planted over large areas, eventually leading to a release from this barrier to invasion. Several species of pine are now highly invasive in South Africa (Van Wilgen and Richardson 2012). A similar dynamic has been observed with native birch and pine trees invading heathlands in England. While these tree species are native, in recent decades they have been gradually invading lowland heathlands where they previously were not found. It has long been postulated that the lack of trees was due to a lack of EM in these ericoid mycorrhizal-dominated areas (Collier and Bidartondo 2009). Collier and Bidartondo (2009) found that individuals can

establish and persist even without their ectomycorrhizal symbionts, but they grow much faster (i.e., are more invasive) once they do establish a mycorrhizal network.

While ectomycorrhizae provide some of the clearest examples of soil suppressing invasion via biotic resistance, arbuscular mycorrhizal fungi (AMF) can also affect exotic invasions. Arbuscular mycorrhizal fungi are generally less host-specific than ectomycorrhizal fungi, so the invasion of exotic plants is typically not completely halted by a lack of AMF as in the case of pines in South Africa (Levine et al. 2004). Instead, exotic invaders often associate with new AMF in the invaded range. There is some evidence that this process may actually delay exotic plant invasion, though not as dramatically as the case of EM species. For example, Jin et al. (2004) found that AMF diversity and infection rate on the invasive plant *Solidago canadensis* increased with increasing time since invasion, suggesting that substantial time was required for *Solidago* to associate with a full complement of AMF fungi. However, the time since invasion in this study was confounded with soil age, since the study was conducted on an alluvial island which was accreting soil and subsequently being invaded. Even if AMF associations are not immediately formed, this limitation may or may not influence the rate of exotic plant invasion. While some studies have shown that newly-acquired AMF associations in the invaded range suppress invasion, in other cases AMF promoted invasion or had no noticeable effect (reviewed in Levine et al. 2004; Shah et al. 2009). This may be in part due to the facultative nature of AMF associations, and also due to variation in the amount of suitable AMF inoculum in the soil (Lekberg and Koide 2005). Some invading plant species may be more reliant on AMF partners than other invaders are, and hence are more affected by a mismatch with AMF in the invaded range. In fact, Pringle et al. (2009) analyzed data on 96 exotic and native plant species from Wilson and Hartnett (1998), and showed that exotics were less affected by AMF than natives. This result would be expected if strong reliance on AMF provided a barrier to invasion. Since the vast majority of land plants form mycorrhizal associations (Wang and Qiu 2006), teasing out the factors that determine when and how AMF and EM suppress or enhance initial establishment and/or subsequent invasive spread could provide a useful contribution to the field.

Not all land plants form associations with mycorrhizae however, and a disproportionately large number of invasive plants are in fact non-mycorrhizal (Daehler 1998). This over-representation of non-mycorrhizal plants might be taken as evidence that exotic mycorrhizal plants are suppressed by a lack of compatible symbionts in the soil. There are two caveats that prevent this conclusion though. First, the majority of non-mycorrhizal exotic invaders are members of just a handful of plant families (e.g., Brassicaceae), so the phenomenon may be at least partially driven by taxonomic bias. Second, disturbed habitats are often colonized by weedy non-mycorrhizal plants, so the overrepresentation of non-mycorrhizal species may simply be a reflection of the high level of invasion in disturbed habitats.

Just as the arrival of mycorrhizal plants before their mycorrhizal symbionts could suppress the initial stages of invasion, the arrival of N-fixing plants before their microbial counterparts might play a role in determining the establishment of an invader. *Falcataria moluccana*, *Cytisus scoparius*, and *Acacia longifolia* all show

evidence of some degree of sub-optimal associations with their N-fixing symbionts (reviewed in Rout and Callaway 2012). However, several lines of evidence suggest that the lack of co-evolved symbionts does not suppress exotic invasion. First, plant families and genera that are predominantly comprised of N fixers (e.g., *Alnus*, *Eleagnus*, Fabaceae) are more likely to be invasive than expected by chance (Daehler 1998), suggesting that N fixers are better invaders than non-fixing plants. Many well-known, notorious invaders are nitrogen fixers (e.g., kudzu, Scotch broom, black locust, acacia). Secondly, N-fixing symbionts are bacterial (*Rhizobium*, *Bradyrhizobium*) or actinobacterial (*Frankia*), which are thought to have lower barriers to dispersal than eukaryotes like fungi (Rout and Callaway 2012). This suggests that exotic plants are less likely to encounter areas where suitable N-fixing symbionts are absent, and many exotic N-fixing plants are not constrained by a lack of symbionts (Birnbaum et al. 2012). Finally, studies suggest that at least some invasive N-fixing plants do not have highly host-specific symbiotic relationships. For example, *Robinia pseudoacacia* associates with at least 5 N-fixing bacterial species from two different genera in its exotic range, some of which were also present in the native range and some which were not (Ulrich and Zaspel 2000). Furthermore, even poorly-matched symbionts can rapidly evolve, resulting in a more adaptive symbiosis (Porter et al. 2011). This low degree of specificity and high plasticity within the N-fixing mutualism means soil biota is less likely to influence the success or rate of invasion through this mechanism (Pringle et al. 2009).

The lack of mycorrhizal or even N-fixing mutualists might suppress or slow invasion during its initial stages, but evidence suggests that eventually this barrier is overcome (Levine et al. 2004) and exotics can then rapidly invade. In both of these cases, the result leads to invasion dynamics reminiscent of the ‘lag’ phase often observed during invasion (von Holle et al. 2003). Many theories have been put forward for the reasons that a lag phase is observed (e.g., Essl et al. 2011; Larkin 2012), but the role of soil biota is not often considered and might be an important mechanism for this phenomenon. There may be cases in which exotic species may establish and become naturalized, but only after the arrival of symbiotic soil biota does the naturalized exotic become invasive. Unfortunately, testing this hypothesis would be quite difficult because very little is known about the movement of exotic soil microbes (Desprez-Loustau et al. 2007, but see Pringle et al. 2009).

These examples discussed above demonstrate how a lack of belowground mutualists might suppress exotic invasion during its initial stages. However, the negative effects of soil biota usually overwhelm the positive effects of mutualisms in natural communities, resulting in net negative effects of the biota in comparisons of sterilized to unsterilized soils (Kulmatiski et al. 2008). Belowground herbivores and pathogens, for example, are a strong force shaping plant community composition (e.g., Mangan et al. 2010). Species-specific herbivores and pathogens are generally less prevalent in the newly-encountered habitats where exotic invasive plants dominate (Mitchell and Power 2003), and this is also generally true for belowground herbivores and pathogens (Callaway et al. 2004). This pattern suggests a large potential for belowground pathogens and herbivores to support exotic invasive plants

by suppressing native plant growth more than exotic plant growth (Bever et al. 1997), and indeed several studies have provided convincing evidence that soils in the invaded range support the growth of exotic plants through belowground enemy release (Agrawal et al. 2005; Klironomos 2002). For example, comparisons of the fungal pathogens present in the native and invaded ranges of several European and North American tree species has shown that the pathogens present in soils from these trees' native ranges have a stronger negative effect on tree seedling mortality than the pathogens present in their invaded range (Reinhart et al. 2010; Reinhart et al. 2003; Reinhart and Callaway 2004).

Though several such examples have shown that soils can and do support exotic plant growth in some cases, not all studies have come to the same conclusion. For example, while Beckstead and Parker (2003) did find strong suppression of *Ammophila arenaria* (Dune beachgrass) in its native range due to belowground soil herbivory, they also found a similar suppression in the exotic range. In a follow-up study, van der Putten et al. (2005) showed that while the suppressive effect of soil biota was generally stronger in the native range, there is a wide range of geographic variation. Understanding what ecological or evolutionary factors give rise to this variation is an important next step in advancing our understanding and could provide new insights into how the soil biota and plant community interact (Perry et al. 2007). Darwin (1859) suggested one possibility; that phylogenetic relatedness between the exotic and the invader would influence invader success due to a larger overlap in shared resources, in this case being enemy-free space. Phylogenetic relatedness does strongly affect overlap in aboveground pathogens (Gilbert and Webb 2007) and insect herbivores (Novotny et al. 2006), so if belowground herbivores and pathogens follow the same pattern, Darwin's hypothesis might help explain some of the geographic variation in the effect of soil biota on invasion. Surprisingly, this hypothesis has seldom been tested (but see Brandt et al. 2009; Dostál and Palečková 2011) and could yield new insights into belowground effects on plant communities.

In addition, because some (though certainly not all) pathogens exhibit some degree of host specificity, plant-soil feedbacks can develop, enhancing the effects of soil biota on plant growth (McCarthy-Neumann and Kobe 2010). For these feedbacks to occur however, plants must have some effect on the abundance and/or community composition of host-specific belowground pathogens. The effects of invasive plants on soils, and therefore also plant-soil feedbacks, will be considered further in the final section of this chapter.

9.1.3 Interactive Effects of Soil Fertility and Soil Biota on Invasibility

Invasibility is widely conceptualized not as an intrinsic property of an ecosystem, but rather as an emergent property which arises as a result of interactions within the ecosystem. Many of the well-studied interactions discussed above are

relatively simple, single-factor mechanisms, but there is an increasing recognition that invasibility is strongly affected by—and likely arises from—complex two-way, three-way, or multi-directional interactions. In many cases, theory provides hypotheses for mechanisms by which soil biota can modulate the simple effects of soil fertility on invasibility, and soil fertility can also modulate the effects of soil biota on exotic plant invasions. Understanding these linkages is an area that is now receiving more attention and is ripe for further exploration.

For example, it is well-established that while mycorrhizae are typically thought of as mutualists, this plant-fungi symbiosis ranges anywhere from beneficial mutualism to parasitism (Johnson et al. 1997; Johnson and Graham 2013; Klironomos 2003). Reducing soil nutrient limitation alters the mycorrhizal fungal community (Egerton-Warburton et al. 2007), shifting the mycorrhizal symbiosis away from mutualism and toward a higher potential for parasitism (Nijjer et al. 2008). Similarly, fertilization shifts the rhizobium–legume symbiosis away from a beneficial mutualism (Lau et al. 2012). Reducing the mutualistic effects of symbiosis has implications for plant community composition and diversity (Collins and Foster 2009), but so far implications for invasibility have received relatively little attention. Nijjer et al. (2008) found that mutualism between AMF and the invasive tree *Sapium sebiferum* was more beneficial to the invasive when fertilizer was added compared to an unfertilized control. This increased benefit of mutualism for the invasive plant was contrasted with three native tree species, which did not benefit more from mutualism in fertilized pots. Grilli et al. (2012) contrasted two co-occurring *Euphorbia* species and found that increasing soil nitrate and ammonium had a stronger negative effect on the AMF colonization of the native *Euphorbia* compared to its invasive congener. Increased nitrate and ammonium also reduced dark septate endophytes in the native, but not in the invasive species. These two studies suggest that the interaction between soil nutrients and mycorrhizae affects the competitive balance between native and invasive plants. It remains to be determined though how widespread or important this interaction is in suppressing or supporting invasive plant dominance or spread.

As noted earlier, escape from belowground pathogens and disease is a major biotic driver of plant invasions that strongly promotes invasion. This aspect of the soil biota also interacts with abiotic conditions in the soil however. Fertilization has been linked to greater plant pathogen loads and reduced resistance to pathogens (reviewed in McKenzie and Townsend 2007). Increased soil pathogen loads could promote invasions by amplifying the effects of belowground enemy escape (Blumenthal et al. 2009). However, if greater nutrient availability increases generalist pathogens which attack invasive species and natives alike, the effects of enemy escape would be dampened. This seems to be the case in aquatic systems, where eutrophication leads to higher loads of primarily generalist pathogens (Marcogliese 2001), but interestingly does not appear to be the case in soils, where evidence points to higher nutrient availability amplifying enemy release (Blumenthal et al. 2009). In addition to these effects on pathogen load, pathogen or herbivore resistance and tolerance can be indirectly affected by nutrient availability via changes in the type and amount of mycorrhizal infection of plants because mycorrhizae influence a plant's

susceptibility to belowground enemies (Kempel et al. 2013; Koricheva et al. 2009). In this way, nutrients can indirectly affect invasion by modifying biotic interactions in the belowground community.

Most research investigating how interactions between resources and soil biota influence invasibility focus on overall mean resource availability, but just as resource fluctuations can directly affect invasions (Davis et al. 2000), fluctuation in resource availability might interact with soil biota in important ways that affect the extent to which soils suppress or promote invasion. Research on microbial responses to fluctuating edaphic conditions has focused largely on pulses of heat, cold, moisture (or lack thereof), and carbon (e.g., Dijkstra et al. 2012), while little is known about microbial responses to nutrient pulses. Since the microbial community mediates nutrient availability to plants (Laungani and Knops 2012), microbial community structure could have important implications for the plant community's response to nutrient pulses. Understanding these implications is an important opportunity to better understand how soil abiotic and biotic attributes jointly influence invasibility.

Similarly, gross N mineralization and the amount of N available to plants (net N mineralization) can differ by an order of magnitude (Laungani and Knops 2012). Understanding how the composition of the soil biota affects competition between plants and microbes for nutrients, and how that might subsequently suppress or support invasive species dominance, is an area ripe for exploration (Chapman et al. 2006; Laungani and Knops 2012).

9.2 Effects of Invasions on Soils and Plant-Soil Feedbacks

Invasive species often dominate large areas, even forming near-monoculture stands of vegetation. Plants and other organisms are one of the five primary state factors driving soil formation (Jenny 1941), so large-scale invasions change the physical, chemical, and biological structure and function of the soil (Ehrenfeld 2003; Liao et al. 2008; van der Putten et al. 2007). This is especially true when invasive species bring novel attributes to the community, such as unique secondary chemicals (Ehrenfeld 2006), new functional traits (Drenovsky et al. 2012; Levine et al. 2003), or new symbionts or pathogens (Pringle et al. 2009; Rout and Callaway 2012). The effects of plant invasions on soil properties has developed into an entire sub-discipline of invasion ecology with several recent reviews (Ehrenfeld 2003; Liao et al. 2008; Pyšek et al. 2012; Vilà et al. 2011) so the topic will not be exhaustively reviewed here. However, many researchers have noted that plant invasions frequently influence the very attributes of soil biology and biochemistry discussed above, and therefore potentially affect the degree to which soils suppress or support their own invasion rate. These reciprocal interactions, or plant-soil feedbacks, between invasive plants and soil are the focus of the remainder of this chapter.

9.2.1 *Feedbacks Between Plant Invasion and Soil Fertility*

Field observations and experiments have shown that there are often larger nutrient pools and fluxes in highly invaded vegetation compared to native uninvaded stands (Liao et al. 2008), and exotic plant invasions can increase soil nutrient cycling (Ehrenfeld et al. 2001; Elgersma et al. 2011; Vanderhoeven et al. 2006), especially when the invasive plant is a nitrogen fixer (Funk and Vitousek 2007; Liao et al. 2008). When high-nutrient conditions favor invasive plants over native vegetation, the increased nutrient pools and fluxes lead to positive feedback in which invasion increases available nutrients, further promoting invasion (e.g., Rodgers et al. 2008). One of the earliest demonstrations of this type of abiotic feedback in the literature is an extensive analysis of the mechanisms underlying the spread of crystalline iceplant (*Mesembryanthemum crystallinum*) in coastal California (Vivrette and Muller 1977). Iceplant accumulates nitrates along with other salts, leading to higher nutrient availability and salinity in soils where it has invaded. This species is also better than native competitors at utilizing the higher nitrate availability in these soils, though this is largely due to its higher salt tolerance. *Carpobrotus edulis*, a closely-related and widespread problematic invader, has similar effects on soils (Conser and Connor 2009). Thus, when these species establish, they “engineer” soils which, due to high salinity, increasingly support subsequent invasion.

Nitrogen fixers such as Acacias and *Morella faya* (*Myrica faya*) invading low-N soils also increase soil fertility, and sometimes this leads to positive feedback when the N-fixer utilizes N more efficiently (Funk and Vitousek 2007) or simply grows larger than natives and thus outcompete natives for light (Holmes and Cowling 1997). In this case, invasive N-fixers engineer soils that indirectly support invasion by shifting competition from belowground to aboveground.

Microstegium vimineum, a C-4 grass, and *Berberis thunbergii*, an understory shrub, are two extremely common forest understory invaders in U.S. eastern deciduous forests, and both species increase nitrification rates when compared to native understory vegetation (Ehrenfeld et al. 2001; Elgersma et al. 2011; Lee et al. 2012; Ross et al. 2011). Both species also show a strong potential for feedback since they grow extremely well in soils with high rates of nitrification and compared to natives, are better able to take advantage of high nitrate availability when grown in monoculture (Elgersma et al. 2012; Lee et al. 2012, but see Ross et al. 2011). Viewed alone, these results suggest that a positive feedback favoring invasion would promote growth and spread of these species. However, competition experiments with natives under varying soil conditions show equivocal support for this conclusion in both cases (Elgersma et al. 2012; Lee et al. 2012). Instead, the higher nitrate availability below these species supports both native and invasive species. Increased nitrogen could shift competition from belowground to aboveground, a shift that could facilitate further invasion (Elgersma et al. 2012), but further work would be needed to determine if this is a mechanism which supports invasion.

The rapid accumulation of litter and soil organic matter beneath many wetland invaders also alters nutrient cycling, leading to higher nutrient availability that

supports the higher invader biomass found in dense invasions (Bills et al. 2010; Tuchman et al. 2009; Currie et al. 2014). The same invasive species which increase litter production and nitrogen mineralization are better able to capture the increased nitrogen than natives, leading to a positive plant-soil feedback (Larkin et al. 2012; Wetzel and van der Valk 1998). The large amount of biomass and litter also strongly shades native competitors, so that light limitation from the dense litter layer and plant canopy also contributes to the dominance of these large wetland invaders (Farrer and Goldberg 2009; Wetzel and van der Valk 1998; Currie et al. 2014).

This set of results highlights the difficult nature of understanding the importance of plant-soil feedbacks. For a nutrient-mediated feedback to support plant invasion, the invasive species must both increase soil nutrients and benefit from those nutrients more than co-occurring natives. Demonstrating these reciprocal effects often requires tightly-controlled greenhouse or common-garden experiments that isolate nutrient effects from other ecological factors. However, as the examples above illustrate, it is often the interactions with light, soil salinity, organic matter accumulation, or other factors that amplify plant-soil feedbacks. By isolating single effects of soil nutrients from competition and other ecologically-important interactions, it is difficult to determine the importance of feedback relative to competition or other ecological factors that come into play in the field (Casper and Castelli 2007; Kulmatiski et al. 2008). When feedback effects are significant but weak relative to other factors or slow to develop, the other factors can override any feedback effects, making them relatively unimportant to the *spread* of invasive plants, though perhaps still important for the *dominance* of invasive plants in areas where they have established (Levine et al. 2004; Suding et al. 2013). However, for many of the cases discussed above, interacting factors (i.e., light limitation, soil salinity) amplify and contribute to plant-soil feedbacks during invasion.

9.2.2 *Feedbacks Between Plant Invasion and Soil Biota*

As noted earlier, soil biota can suppress or promote exotic or native plants, but plants also strongly suppress or promote components of the soil biota as well. This is especially true for soil pathogens or symbionts with strong host specificity. As a result, feedbacks involving host-specific pathogens and symbionts are likely to be stronger than feedbacks involving saprophytic soil biota (Van der Putten et al. 2007), and these feedbacks can be an important component of the invasion process.

For example, while a lack of mycorrhizal mutualists might limit the invasion of exotic species during the initial stages of establishment, once well-established an exotic species can change the mycorrhizal community, potentially affecting native plants and competition between natives and exotics. Non-mycorrhizal invaders such as *Amaranthus viridis* are an excellent example. *A. viridis* is one of several aggressive invaders in the genus, which is generally considered non-mycorrhizal. In areas where *A. viridis* establishes, the availability of AMF spores and propagules is reduced, presumably because *A. viridis* is non-mycorrhizal and therefore reduces AMF host density (Sanon et al. 2012). This reduction in AMF propagules reduces

the competitive ability of co-occurring native plants, leading to greater *Amaranthus* dominance. *Alliaria petiolata*, another non-mycorrhizal exotic invader, not only reduces AMF in this way, it also produces allelochemicals which inhibit AMF spore germination, further disrupting natives' mutualistic relationships (Roberts and Anderson 2001; Stinson et al. 2006). There is also strong evidence that this contributes to *A. petiolata*'s invasiveness in North America, since *Alliaria* has a stronger inhibitory effect on North American plants and AMF than plants and AMF from its native European range (Callaway et al. 2008; Prati and Bossdorf 2004). Similarly, *Centaurea stoebe* reduces AMF diversity and abundance (Mummey and Rillig 2006) and has stronger effects on soil communities in North America where it is invasive compared to its native range in Europe (Thorpe and Callaway 2010). Unlike *Amaranthus* and *Alliaria*, *Centaurea* does utilize mycorrhizal associations during invasion. Thus, reducing the abundance of AMF is not a strategy only for non-mycorrhizal plants, but can be beneficial for mycorrhizal invaders as well. Even invaders with a similar level of mycorrhizal dependence to natives can cause this type of AMF-mediated feedback. When the AMF which are promoted by the invasive species are not as beneficial to resident native competitors, the AMF community promotes further invasion by limiting the growth of native competitors (Vogelsang and Bever 2009; Wilson et al. 2012).

Escape from belowground pathogens and herbivores is one mechanism already discussed by which soil biota can promote exotic invasive plants. Additionally though, exotic invasive plants can alter the belowground pathogen or herbivore communities, potentially leading to feedbacks that influence the rate of invasion. In a modeling study, Eppinga et al. (2006) demonstrated that the growth of exotic species which increase pathogen or herbivore loads is promoted if those exotic species have a high tolerance for pathogens or herbivores, relative to the native plant community. This mechanism was shown to be consistent with data on the invasion of *Ammophila arenaria* in California. Black cherry (*Prunus serotina*), a tree native to North America and invasive in Europe, also follows this pattern. Root-rot pathogens (*Pythium*) isolated from roots in North America and Europe varied in virulence, and pathogens from the invaded range caused less mortality than pathogens from the native range (Reinhart et al. 2010). *Prunus* in the invaded range therefore has a higher tolerance to the pathogens it accumulates, while native competitors may not and could be suppressed by the invader-influenced soil biota.

9.2.3 Feedbacks Driven by Interactions Between Soil Biota and Fertility

The examples above of feedback between the effects of exotic invasive plants on soil biota and subsequent effects on invasion show the importance of interactions with soil biota in the invasion process, but as discussed earlier in the chapter, interactions with soil biota are often modulated by soil fertility. This implies that feedbacks will also depend on the interaction between soil biota and soil fertility. For example, exotic invasive plants that reduce native AMF abundance would only

have a strong indirect effect on native competitors if those competitors rely heavily on beneficial AMF mutualists. In nutrient-rich environments, native plants are likely less reliant on their AMF mutualists, which might even switch to being parasitic under high-nutrient conditions (Johnson and Graham 2013). High-nutrient conditions could therefore interrupt any AMF-mediated plant-soil feedback and prevent its promotion of exotic plant invasion.

Similarly, the strength or direction of pathogen-mediated feedback effects is likely to be context-dependent. High nutrient availability reduces plant resistance to pathogens (McKenzie and Townsend 2007), so changes in nutrient availability could amplify or dampen the strength of pathogen-mediated feedbacks. In addition, nutrient availability affects plant tolerance to enemies due to changes in plant mycorrhizal status (Kempel et al. 2013; Koricheva et al. 2009). Mycorrhizal status affects plant tolerance of belowground herbivory and pathogens, so any change in mycorrhizal status could affect the strength or even direction of plant-soil feedbacks.

Understanding these context dependencies is important for predicting the ability of soil to suppress or promote invasion, and to explain variability in the invasiveness of exotic species across space and time (Blair et al. 2006; Perry et al. 2007). However, most research to date on invasive species' feedbacks has not explicitly investigated interactions between soil biota and soil nutrient availability or variability in feedback strength. This is in part because in order to consider context-dependent variability in feedback strength, feedback experiments need to be repeated in multiple geographical or ecological contexts, something which has not often been done (but see van der Putten et al. 2005; Reinhart et al. 2005). However, a few studies have compared feedbacks in soils with different fertility levels, and some insight may be gained from these studies. Harrison and Bardgett (2010) found very little effect of soil type on feedback strengths when they used previously fertilized or previously unfertilized sandy and clay soils. Similarly, Casper et al. (2008) found little difference in feedback strengths in an experiment conducted using infertile serpentine and fertile prairie soils, although serpentine soils do not necessarily have low nutrient availability and had higher nitrogen (nitrate) availability in their study. In contrast, Manning et al. (2008) found that nitrogen addition modified the strength of plant-soil feedbacks, causing feedbacks to become more negative for some species and more positive for others. Thus, there is a large variation both between and within studies in the degree to which nutrient addition modifies plant-soil feedback. There are many opportunities for further study here to determine the mechanisms underlying these interactions. Understanding these mechanisms may help explain the variation observed between studies to date and improve our understanding of the way soils influence invasion rates.

9.3 Conclusion

Understanding drivers of global change, such as exotic species invasions, is a challenging endeavor that tests the predictive power of ecological theory. The task is difficult because the confluence of many factors determines the success of an invasion,

making invasibility an emergent property of the ecosystem. For plant invasions, many of these factors are regulated by characteristics of soil, and can be attributed in some way to soil fertility, soil biota, and the interactions between them. This chapter describes many of the ways that we understand soil properties promote or suppress exotic invasive plants. In many ways though, soil remains an opaque “black box,” full of uncertainties and incipient discoveries. As new methods and technologies illuminate the unknown, perhaps ecologists will be better equipped to understand and predict the reciprocal influences of soil on exotic plants and of exotic plants on soil.

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Chapter 10

Urban Soil and the Challenges of Restoring Natural Ecosystems

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Abstract Soil properties and their management are often overlooked or underestimated in urban environments, with native vegetation stands and agricultural fields replaced by buildings and roads. Soil physical properties such as bulk density and porosity are altered through crusting, compaction, or artificial soil sealing by heat-absorbing, impervious surfaces of asphalt and concrete. These physical changes are also deleterious to soil water infiltration, aeration and percolation, and result in increased runoff. In urban catchments, sediment and nutrient-enriched alkaline stormwater runoff is often directed to the soil of retained remnant vegetation patches.

The soil physical and chemical changes adversely affect soil microbial activities and natural nutrient cycling. The colonisation of the remnant native vegetation in urban environments by common worldwide weeds are symptomatic of these changes. Increasingly at risk of extinction are the native species and ecosystems of the remnants in the formerly distinct local climatic and soil conditions. The challenges of protecting, restoring and/or maintaining the native remnants are dependent on an understanding of the soil-plant interactions and implementation of measures to mimic pre-development conditions.

10.1 Introduction

Soil properties and their management traditionally studied in a rural or semi rural context, are often overlooked or underestimated in an urban environment (Hazelton and Murphy 2011).

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More than 8,000 years of human induced changes to native ecosystems has preceded urbanisation (DeFries et al. 2004, 2012; Ellis 2011; Syvetski and Kettner 2011; Pavao-Zuckerman and Byrne 2009; Grimm et al. 2008). The increase in population in urban areas has resulted in compact cities expanding rapidly into peri-urban fringes (Piorr et al. 2011; Pickett et al. 2001). Native vegetation and agricultural land is being converted to urban or suburban land use at a higher rate than the growth of urban populations. This trend is also occurring throughout Asia. In China, for example, Nanjing City's population has increased eight fold from approximately 700,000 in 1949 to almost 5.5 million by 2009; during the same time period the urban area has increased 14-fold from approximately 42–577 km² (Wei et al. 2013). Over the next several decades it has been predicted that nearly all population growth in the developing world will occur in urban areas (DeFries et al. 2012; Grimm et al. 2008). Land previously considered to be of environmental risk from flooding, coastal erosion and bushfires, has become increasingly urbanised over the past 50 years (Millennium Assessment 2005).

Soils affected by urban processes differ from non-urban soils chemically, physically and biologically (Hazelton and Murphy 2011; Pouyat et al. 2007a). The obvious changes that accompany urbanisation are an increase in heat-absorbing, impervious surfaces and the replacement of native vegetation or agricultural fields with buildings, roads, lawns and gardens (Wei et al. 2013; Wright et al. 2011; Davies et al. 2010; Kaye et al. 2006; Biasioli et al. 2006; Lemus et al. 2004).

Physical soil properties such as bulk density and porosity are altered through crusting, compaction or artificial soil sealing by asphalt and concrete. These physical changes are deleterious to soil water infiltration, aeration and percolation. In Nanjing City, soil samples were collected by Wei et al. (2013) under impermeable pavement from eight sites, including roads, residential paved squares and alleys. As a control, two sites with similar soil parent material were selected from open soil. It was found that urban sealing significantly decreased the contents of soil organic matter, from 6.5 g/kg under impermeable pavement compared with 18.5 g/kg in open soils. Likewise fine earth microbial biomass C and N (C_{mic} and N_{mic}), which affect nutrient availability, were greatly affected by sealing of the soil, with the C_{mic} fine earth contents being 55.8 mg/kg compared with 317.9 mg/kg in open soil. The soil N_{mic} values varied between 5.6 and 79.3 mg/kg, and differed greatly among land-use types in sealed roads and between the open and sealed roads (Wei et al. 2013).

Stormwater runoff from urbanized surfaces collect nutrient loads such as nitrogen and phosphorus as well as other contaminants (Paul and Meyer 2001; Young and Young 2001). Phosphorus is found especially in older urbanization situations (Carpenter et al. 1998). In Moscow, for example, a thick cultural layer richer in nutrients than the natural soil has developed towards the centre of the city (Hazelton and Murphy 2011; Stroganova et al. 1998). The increase in nutrients has been attributed to the accumulation on the soil surface of different materials resulting from human activities (Hagan et al. 2012; Hazelton and Murphy 2011; Stroganova et al. 1998).

The impervious concrete surfaces and drains in urban areas increases the alkalinity of the stormwater (Davies et al. 2010). In Torino, Italy, for example, urban soils

were found to be mostly neutral to alkaline with a mean pH of 7.2. In contrast nearby rural soils had a pH ranging from 3.7 to 8.0 with a mean of 5.6 (Biasioli et al. 2006). In contrast, the increased use of cars and industrial emissions increase soil acidity (Hazelton and Murphy 2011).

Soil chemical and biological properties can also be affected by the concentration of contaminants from residential and industrial complexes. Pollutants such as lead persist in soil, despite leaded petrol being phased out in the early 2000s and leaded paints being gradually phased out from the 1970s (Hazelton and Murphy 2011; Snowden and Birch 2004; Markus and McBratney 2001; Stroganova et al. 1998). Elevated metal concentrations, especially from former industrial sites, can reduce soil microbial biomass levels and inhibit nitrogen fixation by both free-living and symbiotic organisms, hence altering soil food webs, decreasing decomposition rates and shifting biogeochemical cycling of urban soils (Pavao-Zuckerman 2008; McGrath 1994). For example, from seven points along a gradient in close proximity to a copper smelter in Zhujiawu in China, Wang et al. (2007) found that C_{mic} was negatively affected by the elevated heavy metal levels and was closely correlated with heavy metal stress. Elevated metal loadings resulted in changes in the soil microbial activity with enzyme activity greatly depressed in the heavy metal-contaminated sites.

A direct outcome of urbanisation is social interaction and an increase in recreational facilities including parks, playing fields and golf courses. Sometimes these facilities are developed on totally altered land, such as “cut and fill” or on former landfill emplacements that have been capped with compacted clay and covered with layers of sand and grass turf. Severe interface problems from introduced “fill” topsoil on “in situ” subsoil can cause poor infiltration resulting in sparse or no vegetation growth (Handreck 1994). In these circumstances it may be necessary to use a man-made soil. As an example, for the successful construction of a golf course there are specific soil requirements for greens and tees as well as artificial subsoil drainage. Man-made soil mixes are generally used in the root zone to achieve the required 35–55 % total porosity, 15–30 % air-filled porosity, 15–25 % capillary porosity and a minimum of 150 mm/h saturated hydraulic conductivity (Moore 2004).

At five UK golf courses, the different construction materials and maintenance regimes for the tees, fairways and greens resulted in different soil microbial communities (Bartlett et al. 2007). It was also determined that the construction and maintenance of specific areas of a golf course reflected the physicochemical status of the microbial habitat, irrespective of geographical location (Bartlett et al. 2007).

The altered soil physical and chemical properties in urban and suburban environments has changed the natural ecosystems and biodiversity (Wei et al. 2013; Zhang et al. 2007; Burghardt 2006) with the evolution of distinctly different urban ecosystems (Kaye et al. 2006). Another effect of continued population growth and the expansion of residential areas is land clearing, resulting in “islands” of remnant vegetation or occasional trees of the original vegetation being surrounded by suburban development (Charman 2007; Benson and Howell 1990). As a consequence, native ecosystems worldwide are being listed as threatened (critically endangered, endangered and vulnerable analogous to the International Union for Conservation of Nature criteria

for species (Wyse Jackson and Kennedy 2009; Nicholson et al. 2009; Preston and Adam 2004)). The long-term survival of retained native ecosystems in urban environments are at risk from the resultant urban soil changes.

The challenge of maintaining, protecting and/or restoring these native remnant ecosystems is to re-establish, protect and mimic pre-development soil landform, structure and function (Pavao-Zuckerman 2008). For successful ecosystem re-establishment, an understanding of soil/plant interactions, as well as understanding of the often city-specific distinct soil chemical signatures associated with climate, geology and land use, are essential (Ellis 2011; Heneghan et al. 2008).

10.2 Case Study – Sydney, Australia

In Australia the pattern of settlement of the first European colony was related to the distribution of the soil. Although the harbour site was chosen because of the availability of freshwater, the “luxuriant prospect of its shores, covered with trees to the water’s edge” (Tench 1789; Clark 1963) also appeared to be indicative of fertile soil. Extensive clearing of the native vegetation followed. Almost immediately it became evident that although the sandy soil supported lush native vegetation it was unsuitable for agriculture (Perry 1963). Urgent expeditions eventually discovered areas of fertile silty loam soil better suited to agriculture and these had the highest native vegetation clearance rates (Corey Bradshaw 2012; Braithwaite 1996; Benson and Howell 1990; Bannerman and Hazelton 1990; Chapman and Murphy 1989). In contrast, the native vegetation of the shallow sandy soils and steep terrain remained relatively intact. National Parks were declared in the 1890s in these areas to the south and north of Sydney (Hazelton and Clements 2011).

In the nineteenth and early twentieth centuries, urban expansion occurred largely on the previously cleared, more favourable agricultural soil on the hilltops and adjoining upper slopes (Hazelton and Clements 2011; Benson and Howell 1990; Spearitt 1978). By the 1950s, urban development extended onto the vegetated sandstone slopes often adjoining steeper gullies and also spreading onto the alluvial floodplains (Hazelton and Clements 2011) with the increased risks of bushfire and inundation respectively.

Today the “islands” of original native vegetation, often “protected” in parks and reserves, are threatened by nutrient and sediment-enriched run-off from gardens, roads and roofs, as well as altered fire regimes related to protection of urban assets (Charman 2007; Benson and Howell 1990; Clements 1983). Elevated phosphorus levels as high as 438 ppm have been recorded near urban stormwater outlets in sandstone-derived soils, compared with natural phosphorus levels of 20–40 ppm in non-urban sandstone-derived soils (Leishman 1990).

To determine the effects of urbanisation on native vegetation remnants, soil pH, soil nutrient levels and species composition were recorded by Clements (1983) in three replicates in four physiographic locations (hilltops, north facing

slopes, south facing slopes, and valleys), on two main soil types (shale-derived and sandstone-derived) and two urban-site types (surrounded by suburban development and relatively unaffected). The pH of urban shale-derived soil (pH 4.8–7.2) and urban sandstone-derived soil (pH 3.9–7.5) was up to two units higher than of non-urban shale-derived soils (pH 4.8–5.5) and non-urban sandstone-derived soils (pH 4.3–5.2). The increase in pH levels alters the availability of soil nutrients with phosphorus being more soluble at higher pH levels (Tisdale and Nelson 1993; Charman 2007). The total soil phosphorus levels in urban sites were on average approximately 50 ppm higher than in non-urban sites for both shale- and sandstone-derived soils. The total soil phosphorus levels of the sandstone-derived soils in urban areas were similar to those of non-urban shale-derived soils (approximately 80–90 ppm on the slopes). Clements (1983) found in remnant vegetation patches that the increases in soil moisture were proportional to the non-porous surface in the catchment and that soil nutrient had increased due to urban impacts. There were decreases in species richness and in abundance of the locally indigenous sclerophyllous species, typical of dry sclerophyll forests and heaths. There were also increases in abundance of native mesomorphic species typically associated with wet sclerophyll forests and rainforest margin habitat as well as exotic common worldwide weed species.

Gullies receiving urban run-off are particularly susceptible to increases in soil moisture and nutrients, resulting in species compositional changes (Benson and Howell 1990; Clements 1983). The high-rainfall areas on shale-derived soil in northern Sydney once supported a valuable source of timber resource with trees over 40 m in height. This forest type, once dominated by *Eucalyptus saligna* (Sydney Blue Gum), and now listed as the critically endangered ecological community Blue Gum High Forest, is now often reduced to canopy trees and largely restricted to steep-sided urban head gullies. In a suburban head gully supporting this community, AnneMarie Clements in 2012 recorded the canopy trees being smothered by common worldwide weeds including the exotic climber *Ipomoea indica* (Blue Morning Glory) with up to 50 % projected foliage cover, *Lantana camara* (Lantana) with up to 80 % cover and by *Ligustrum* spp. (Privet) with up to 80 % cover. The nutrient cycling of these exotic species differs from that of eucalypts that evolved in nutrient-limited environments (Wardle et al. 2004). In eucalypts, prior to litter fall, a large percentage of nutrients is withdrawn from the senescent leaves to the living tree (Attiwill et al. 1978, 1996).

The foliage phosphorus concentrations of these exotic species in northern Sydney gullies exceeds 1,000 ppm (Lambert and Turner 1987). These concentrations are attributed to nutrient-enriched urban stormwater. For example, under dense *Lantana camara*, pH, total nitrogen and phosphorus, and available nitrogen and phosphorus are significantly higher than corresponding levels 2–5 m away from the *Lantana* individuals (Fan et al. 2010). The invasion by exotics such as *Lantana camara* in disturbed forest results in a feedback system that accelerates *Lantana* spread by promoting its competitive superiority in the enriched nutrient environment over native species (Sharma and Raghubanshi 2010; Gooden et al. 2009a, b; Richard Lamb's unpublished research discussed in Buchanan 1989).

Increases in soil moisture and nutrient-enrichment, and associated displacement of remnant native vegetation by common worldwide weeds in urban environments, places remnant native ecosystems at risk of extinction in the Sydney area.

10.3 Conclusions

Urbanisation has replaced native vegetation and agriculture fields, with heat-absorbing, impervious surfaces and increased contaminated sediment and nutrient-enriched alkaline stormwater runoff. The resultant changes in the physical and chemical soil properties adversely affect soil microbial activities and natural nutrient cycling, resulting in colonisation of remnant native vegetation by common worldwide weeds.

The challenge of protecting, restoring and/or maintaining native remnant vegetation is dependent on understanding of the soil-plant interactions. The implementation of measures to mimic pre-development conditions of landform, soil moisture content and nutrient cycling is essential for effective management of urban soil, the importance of which at present, is underestimated.

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Chapter 11

Toward a Holistic Approach to Soils and Plant Growth

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Abstract We propose that a holistic view be taken to the study and implementation of ecological research into soils, soil organisms and plant growth. This builds upon the spatial and temporal aspects of soil physical and biological characteristics at the micro- and macroaggregate scales. This has major implications for the interactions of the soil biota and also for the possibilities of soil organic matter (SOM) dynamics, including gradual accumulation of SOM across decades and centuries. One of the key integrating factors in the role of soil biota in plant nutrition is the centrality of detrital and soil food webs in fostering nutrient cycling and ecosystem stability. We conclude with a five-dimension approach to studying key factors in soil biological interactions that affect plant nutrition and also long-term carbon balance in natural and agricultural ecosystems.

11.1 Introduction

In this second decade of the twenty-first century, a majority of the scientific world and the principal user groups (e.g., agriculturists, foresters, horticulturalists) frequently view soils as black boxes, merely providing inputs of tillage and fertilizer to them, and waiting for beneficial outcomes. The outcomes are occasionally what the users intend, but often at considerable cost compared to a more-informed

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approach. This chapter summarizes several avenues forward out of what is currently an impasse in soil biology and ecology.

As the nature and extent of soil biodiversity is more widely appreciated, particularly in the incredibly speciose area of microbial communities, there has been a temptation to focus almost exclusively on this area of soil biodiversity. As is noted in several of the chapters in this book, this basic knowledge is fascinating and important in its own right (Whitman et al. 1998). However, we suggest that a more holistic approach, including multi-trophic interactions (Havlicek and Mitchell, Chap. 2; Hazelton and Clements, Chap. 10), focusing on soils as true organizing centers of terrestrial ecosystems (Coleman et al. 1998) will pay major dividends in the future.

By emphasizing plant-soil-microbial-faunal interactions, including the increasing awareness of the key role of viruses in soils, this enables the investigator and farmer-grower to take a longer-term approach (Dighton, Chap. 1; Kimura et al. 2008; Guénola, Chap. 5). This topic is emphasized in Coleman (2011) and Van der Putten et al. (2009). We suggest that the best way to proceed successfully is to treat soils and the biota within them as an n-dimensional hypervolume, *sensu* Hutchinson (1957), by allowing soils to develop, biologically and pedologically, over time, including evolutionary dimensions as well.

11.2 Temporal and Spatial Dimensions of Soil Ecology

One of the recurrent themes in this book is the need to achieve a synthesis between shorter-term process studies and longer-term evolutionary studies, in a soils context. Thus whether studying phenomena at the soil micro- and macro-aggregate level, the rhizosphere, and other areas of significant activity (so-called “hot spots”), we need to study the mechanisms over short-term days to weeks, and longer-term months to years to decades in a pedological context (Coleman 2008; O’Brien and Jastrow 2013). One significant benefit of this approach is to enable soils to begin storing significant amounts of soil organic matter, which will be an important benefit gained from treating agricultural and forested soils in long-term fashion, facilitating oxygen and transport in soils. This has considerable bearing on the production and uptake processes of the major greenhouse gases (Blagodatsky and Smith 2012). This long-term approach will literally enable the soils to “work for us”, *sensu* Elliott and Coleman (1988).

A principal reason for being concerned with the time course of micro- and macroaggregate formation is the increasing concern with the phenomenon of soil carbon saturation, in the context of global climate change (Stewart et al. 2007, 2008). Working with “nested” models should provide some useful insights into evolutionary pedology (Yoo et al. 2011; O’Brien and Jastrow 2013) develop the concept of hierarchical soil aggregates, regulating soil C and N recovery in restored perennial grasslands. They isolated particulate organic matter (POM) and silt- and clay-sized fractions from four defined locations within soil collected from an agricultural field, prairies restored for 3–33 years, and a never-cultivated remnant prairie. They then

used aggregate hierarchy to define their four soil locations: non-aggregated material, free micro-aggregates, macroaggregates (excluding encapsulated microaggregates), and microaggregates within macroaggregates (Jastrow et al. 1998). They found that the duration of linear soil C and N accumulation differed among aggregate-occluded pools in relation to the combined influences of soil mass redistribution and increases in C and N concentrations. Even after several decades, silt in microaggregates isolated from within macroaggregates contributed the greatest quantities of C and N to whole soil, yet reached steady state C and N contents that were only 59 % and 56 % for C and N respectively, of those observed in the reference remnant prairie soil. O'Brien and Jastrow (2013) noted that the pools fell short of the original levels but seemed to reach steady state at the time of sampling. They postulated that several "transient steady states" could occur in some SOM pools along the way to an overall whole-soil steady state that might take centuries to achieve.

Studies of the conjoint interactions of microbes, fauna, and root and leaf litter inputs, via detrital food web models, have been very informative and productive of new insights into system-level phenomena. The importance of plants and soil biota to soil formation and processes has been understood for more than a century (Darwin 1881; Jenny 1941). Plants introduce organic substrates into soils as products of growth, senescence and death, while soil microbes and invertebrates utilize these organic substrates as an energy source and in the process contribute their own organic substrates through consumption, growth and death. For microbes the dominant constituents include microbial cell wall residues and hyphae in the case of fungi, extracellular polysaccharides, carbohydrates, and amino sugars (glucosamine, galactosamine, and muramic acid). For invertebrates the substrates include nitrogen rich fecal pellets, cell walls, chitinous exoskeletons, cytoplasm, and mucus secretions (Coleman et al. 2004).

Apart from the transformation and direct inputs of organic substrates, soil invertebrates indirectly affect the decomposition of organic substrates by enhancing the activities of soil microbes through grazing, comminution, and dissemination (Wallwork 1976; Moore et al. 1988). Moderate levels of consumption of microbes by protozoa and invertebrates can stimulate further microbial growth through the principle of optimal grazing (Hilbert et al. 1981; Clarholm 1985; Wall and Moore 1999). Assuming that microbes exhibit logistic growth tied to available resources with a carrying capacity K , microbial growth rates are maximized at population densities of $K/2$. Higher growth rates translate to increased utilization and transformation of organic substrates and increased production of microbial-derived organic substrates. Given that most invertebrates consume more nitrogen than they require for growth (i.e., invertebrates are net mineralizers of nitrogen), enhanced microbial growth through grazing leads to increased nitrogen availability for plants. When this process plays itself out within the rooting zone of plants, a positive feedback can occur wherein plants and the soil food web feed off one another's excess and waste. Under this scenario, plants exude excess photosynthate in the form of labile carbon substrates from their roots, which in turn are utilized by microbes and subsequently as food for microbivorous invertebrates, which release nitrogenous waste that is utilized by plants (Gupta et al. 1999; Ingham et al. 1985).

Many invertebrates feed directly on plant materials and organic substrates. The fragmentation or comminution of these materials enhances their decomposition. For plant structural materials, comminution increases the surface areas of the materials and exposes cytoplasm, thereby enabling greater access by microbes. Decomposition is further accelerated as the feeding activity often results in the translocation of nitrogen from the soil to the substrate in the form of fecal material and through fungal hyphae. Grazing by invertebrates disseminates microbes from one organic source to another as many microbes adhere to invertebrate exoskeletons and cuticles and survive passage through their digestive tracts (Coleman et al. 2012).

11.3 An Integrative Framework

A framework that links soil microbes and invertebrates as described above, directly to pedogenic processes, is beginning to emerge. Soil food webs and the differences in microbial and invertebrate life forms within them offers a starting point to connecting the components of the detrital food web to soil pedogenesis and SOM dynamics (Coleman et al. 1983, 2004). Coleman et al. (1983) identified a bacterial-based fast cycle and fungal-based slow cycle within soils. Subsequent studies revealed that these fast cycles and slow cycles were borne from the trophic interactions of detritus to bacteria and their consumers and from detritus to fungi and their consumers (Hunt et al. 1987; Moore et al. 1988; De Ruiter et al. 1996). These dominant trophic pathways, or 'energy channels', are ubiquitous across ecosystem types and grounded in the basic architecture of soil food webs and their structural stability (Moore and Hunt 1988).

These detrital food webs can be condensed into the dominant pathways beginning with pools of detritus or soil organic matter that differs in quality. These pools would serve as the primary energy sources for a suite of bacteria and fungi, each of which is consumed by a host of microbial consumers and predators. Metabolic wastes and byproducts that cycle back as energy sources and binding agents would be factored in much as C and N are in the current generation of models. This approach preserves the basic premise of material transformations that occur in the soil carbon models (Parton et al. 1987; Gijsman et al. 2002) and material transfers that occur in food web models (Hunt et al. 1987; De Ruiter et al. 1993; Fu et al. 2000) in a way that provides a common currency. Moore et al. (2003) presented a first approximation of this approach by linking the activities of organisms within the bacterial and fungal pathways to SOM dynamics and key ecosystems processes. Here, SOM is broadly defined as non-living organic material within soils, regardless of form or origin (e.g., detritus, dead roots, corpses of soil biota, traditional SOM). The balance in the activities of one pathway relative to the other is governed by the quality of SOM, with low C: N (<30) substrates favoring the bacterial pathway and high C: N (>30) substrates favoring the fungal pathway. This model allows for changes in the relative activities of the different pathways with natural seasonal variation in the phenology of plants and season succession in plant types, as well as

abrupt or gradual changes that result from different land-use practices and increases in atmospheric CO₂. Fu et al. (2000) viewed the whole soil food web as a 'super-organism' and considered that organisms at different trophic levels work together to process SOM but with various strategies and turnover rates.

Global experiments and syntheses have continued to address the quantification of the role of soil fauna in ecosystem processes and in particular, have led to increased evidence for their contribution to C cycling. Global multi-site experiments show that soil fauna are key regulators of decomposition rates at biome and global scales (Wall et al. 2008; Powers et al. 2009; Makkonen et al. 2012). Garcia-Palacios et al. (2013) conducted a meta-analysis on 440 litterbag case studies across 129 sites to assess how climate, litter quality, and soil invertebrates affect decomposition. This analysis showed fauna were responsible for ~27 % average enhancement of litter decomposition across global and biome scales.

Agricultural practices affect many of the key functional and structural attributes of ecosystems in several ways: the transformation of mature ecosystems into ones that are in a managed developmental state are induced by tillage operations and other activities such as applying fertilizers and pesticides. These manipulations have the potential to shift the elemental balance of a system and decrease species diversity and alter the soil food web (Cheeke et al. 2012; Moore and de Ruiter 2012). Conventional tillage practices alter the distribution of organic material and affect the rate of formation of micro- and macro-aggregates in the soil profile. This has a profound effect on the turnover rates of organic matter that is associated with the aggregates (Elliott and Coleman 1988; Six et al. 2004; O'Brien and Jastrow 2013) as well as affecting ecosystem services (Cheeke et al. 2012). De Vries et al. (2012) showed that grassland, fungal-based, food webs were more resilient than agricultural fields with bacterial-based food webs, and provided evidence for management options that enhanced ecosystem services. Similarly, a conservation management seemed to be helpful for the development of Eucalyptus plantations in South China. The understory fern (*Dicranopteris dichotoma*) was found to contribute substantially to sustain fungal population and enhance litter decomposition in Eucalyptus plantations of south China (Wu et al. 2011; Zhao et al. 2013), although it showed less influences on the total soil microbial biomass and nematode abundance (Zhao et al. 2011).

We proposed that the biotic processes in the plant-soil biota-soil mineral system may be controlled primarily by the distribution patterns of readily favorable resources (i.e., could be used with lowest cost) among plant, soil biota and the soil minerals. One of the key characteristics of the readily favorable resources for a given biotic form is that the elemental balance (e.g., C, N, P ratio) of resource is as close as the balance of the user. The growth of plant and soil biota was then affected similarly by the difficulty of keeping the elemental balance. For instance, both plant and soil microbes need to increase the energy input when they require more nutrients, or need to deal with resource-depleted habitats. On one hand, Yi et al. (1995) found that the turnover rate of soil microbes in plantations (with low soil fertility) were usually higher than that in mature forest (with high soil fertility) in south China. This suggested that soil microbes used more energy to sustain the same level of

growth in harsh environment than under favorable conditions. On the other hand, Yin et al. (2013) found that plants secrete more root exudates to stimulate soil microbes to enhance mineralization only in forest with low nutrient content in response to elevated CO_2 . This may be because that plant has to activate and absorb more nutrients in response to a higher carbon fixation when CO_2 was elevated; and the extra root exudate is the cost of keeping the elemental balance. In contrast, plants could easily obtain enough nutrients in forests with high nutrient content to keep the elemental balance; as a result, less root exudate was produced in response to elevated CO_2 . Soil invertebrates such as earthworms may affect the plant-microbial association by increasing the carbon and nutrient availability and, then enhance the energy utilization efficiency of both plants and soil microbes. Overall, an increased absorption of certain elements in plant or soil biota, as a consequence of the global change or human disturbance, will result in increases of other related elements; otherwise the growth of plant or soil biota may be hampered, or they would evolve to adapt a new elemental balance, i.e., changing their elemental ratios. What we need to know are which balance is optimum among plants, soil microbes and soil invertebrates and how to keep this balance, so that each component could obtain enough carbon and nutrients in time and the associated energy cost may be as low as possible.

If we recognize a well-developed natural system as the reference which is so-called “optimum balance”, the next step is to know the contribution of each major component to those key ecological processes in this reference system so that we could regulate the target system accordingly. However, it is difficult and the results may often contradict each other. As an example, here we show how earthworms contribute to net carbon sequestration in soil. Earthworms were often found to stimulate CO_2 emission, especially in short-term experiments, but they have also been reported to enhance carbon stabilization in soil aggregates in some longer-term experiments. Nevertheless, more experimental data support the view that earthworms reduce carbon sequestration due to the fact that CO_2 emission is easier to detect than carbon stabilization. As a result, a recent meta-analysis study concluded that earthworm presence will increase CO_2 emissions from soil by 33 % (Lubbers et al. 2013). In contrast, Zhang et al. (2013) found that earthworms could facilitate net carbon sequestration through unequal amplification of carbon stabilization compared with carbon mineralization. Zhang et al. proposed that neither an increase in CO_2 emission nor that in stabilized carbon would entirely reflect the earthworms’ contribution to net carbon sequestration; that is, the impacts of earthworms on the two coupled processes of carbon mineralization and carbon stabilization should be studied simultaneously. They found that, firstly, although earthworms accelerate carbon mineralization, the total amount of CO_2 that can potentially escape from the soil with earthworms differs little from soil containing no earthworms because the capacities of carbon mineralization of earthworms and soil microbiota are similar. Most previous studies did not note this and, thus, were likely to conclude that earthworms decrease carbon sequestration only because CO_2 emission was often enhanced by earthworms. Secondly, given that an increase in carbon mineralization (C_{min}) and carbon stabilization (C_{sta}) may be a natural consequence of an increased

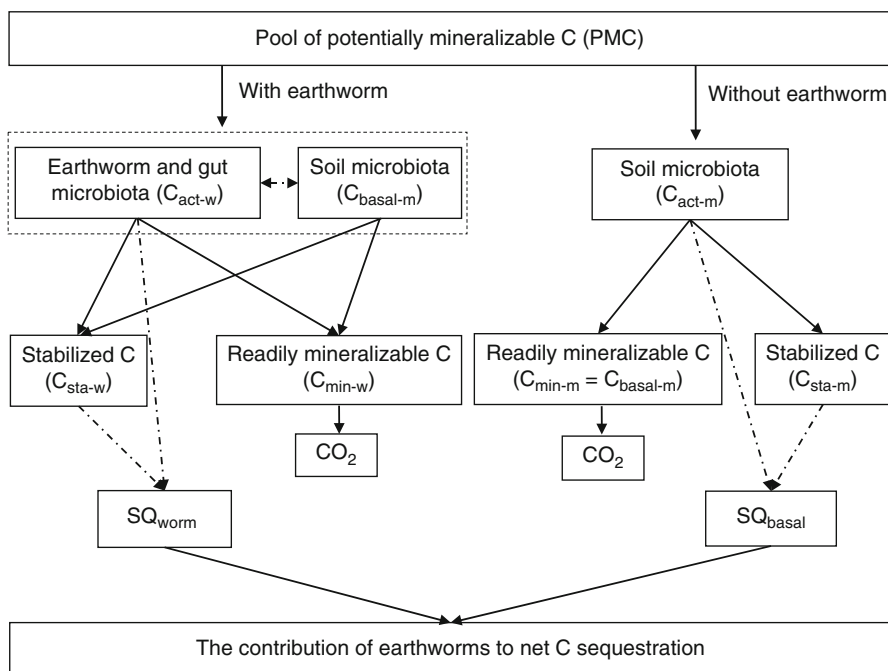


Fig. 11.1 A conceptual model of how earthworms regulate C sequestration. C_{act-w} and C_{act-m} refer to the earthworm-activated and soil microbiota-activated mineralizable C, respectively. C_{min-w} and C_{sta-w} refer to the pool of readily mineralizable C and pool of stabilized C in soil with earthworms, respectively; C_{min-m} and C_{sta-m} refer to the pool of readily mineralizable C and pool of stabilized C, respectively in soil without earthworms. Given that the soil microbiota-induced readily mineralizable C (C_{min-m}) may also be metabolized and/or stabilized by earthworms, C_{min-m} is also defined as basal C ($C_{basal-m}$). Note that the value of C_{min-m} ($C_{basal-m}$) in a system with and without earthworms may gradually differ as earthworm incubation proceeds. C_{sta-w} and C_{act-w} are the differences between C_{sta} and C_{sta} plus C_{min} between soil with and without earthworms, respectively. SQ_{worm} and SQ_{basal} refer to the C sequestration quotient in soil with and without earthworms, respectively. The *single-ended dot-dash lines* represent the major components for the calculation of SQ values. The *double-ended dotted line* indicates possible interactions (This figure was from Zhang et al. (2013))

pool of activated carbon, the pool size of the activated carbon (C_{act}) and its allocation pattern into carbon mineralization and carbon stabilization then determine the net carbon sequestration. Thus, Zhang et al. introduced the new concept of sequestration quotient ($SQ, C_{sta}/C_{act}$) to quantify the earthworms' impact on the balance of carbon mineralization and carbon stabilization (Fig. 11.1). The study revealed that the presence of earthworms is more likely to create a carbon sink as the carbon stabilized by earthworms outweighs that converted to CO_2 during carbon mineralization, i.e., SQ values are higher in soil with earthworms (Fig. 11.2a, b). Importantly, the patterns of CO_2 emission and net carbon sequestration are predictable by comparing SQ values between treatments with and without earthworms (Fig. 11.2c). Apparently, the concept of SQ could also be used to estimate the contributions of

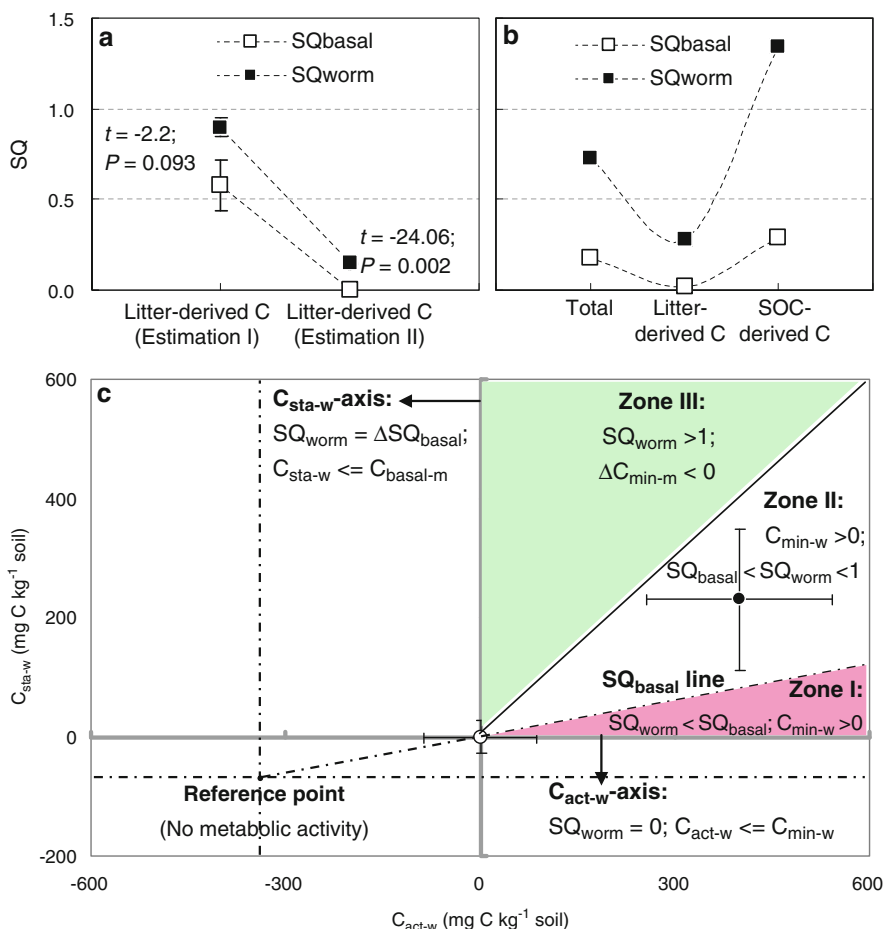


Fig. 11.2 Sequestration quotient and its connection with C sequestration. The sequestration quotient (SQ) in phase II (a) (mean \pm s.e.m., $n=3$) and in the literature (b), and the conceptual diagram (c) showing how to predict the impacts of earthworms on CO₂ emission and net C sequestration with SQ values. The s.e.m. is indicated by error bars. Earthworms converted the PMC into readily mineralizable C, and protected a larger proportion of readily mineralizable C. SQ_{worm} (closed squares) and SQ_{basal} (open squares) values were calculated to quantify the balances between C mineralization and C stabilization in soil with and without earthworms, respectively. Estimation I: all litter-derived C in soil aggregates were assumed to be stabilized; estimation II: about 17 % of litter-derived C in microaggregates within large macroaggregates and only 8 % of litter-derived C in microaggregates were assumed to be stabilized for soil with and without earthworms, respectively (Bossuyt et al. 2005). In (c) the two dot-dash axes represent the reference x-axis and y-axis in control soil without earthworms; the origin of the dot-dash axes refers to a reference point of no metabolic activity. The two bold grey axes represent the x-axis and y-axis in soil with earthworms, namely the net effects of earthworms on C activation (C_{act-w} -axis) and C stabilization (C_{sta-w} -axis); Zones I, II and III indicate the three major scenarios of the contribution of earthworms to C sequestration. The open white circle, i.e., the origin of the bold grey axes (C_{act-m} , C_{sta-m}), refers to the mean values of C_{act-m} and C_{sta-m} in control soils, i.e., the basal point. The closed black circle (C_{act-w} , C_{sta-w}) refers to those values in soils with earthworms. Data are the same as presented in panel (a) and (b). C_{sta-m} or C_{min-m} and C_{sta-w} or C_{min-w} refer to the soil microbiota-induced and earthworm-induced C_{sta} or C_{min} , respectively. Since part of C_{min-m} may be metabolized and/or stabilized by earthworms, C_{min-m} is also defined as basal C ($C_{basal-m}$). Note that the conversion rate from PMC to C_{min-m} and C_{sta-m} may also be affected by earthworms, thus the value of C_{min-m} ($C_{basal-m}$) in a system with and without earthworms may gradually differ as earthworm incubation proceeds (This figure was from Zhang et al. (2013))

other factors/treatments (not only earthworms) to net soil carbon sequestration and the related nutrient cycling. However, note that the net contributions of earthworms to carbon cycling at ecosystem, regional or global scale are still hard to quantify. The primary difficulty is the response and feedback of other components (e.g., plant growth) associated with earthworms' alteration of the ecosystem are scarcely known. For instance, earthworms interact with plant species and impact plant productivity of the sites, which cause feedback on carbon sequestration at the time scale of years to decades or even longer. It is thus unlikely that a short-term study can determine the actual amount of carbon being sequestered by earthworms in the field. On one hand, the earthworm-stimulated CO₂ emission may be partially offset or even overcompensated by carbon sequestration resulting from plant uptake if net primary productivity (NPP) increases in response to nutrients released by the accelerated mineralization (Edwards and Bohlen 1996). On the other hand, plant productivity may be reduced and thus results in negative feedback on the amount of carbon that earthworms can sequester if a significant proportion of the nutrients that earthworms liberate from leaf litter or SOC is leached away.

In brief, there are five major relationships in the plant-soil system: (1) one component functions as a basic condition (such as platform) which supports other components or processes but its level does not affect the magnitude of those latter components or processes. For example, the role of understory ferns in Eucalyptus plantations of south China is more likely to provide a suitable microenvironment for soil biota rather than as a food resource. (2) One component exerts ascertained impact on other components or processes either positively or negatively. For example, soil microbial biomass increase with soil fertility, while the turnover rate of soil microbes declines with soil fertility. (3) One component affects other components or processes positively through one way and negatively through other ways. For example, nematodes may reduce microbial biomass by grazing but also facilitate the dissemination of soil microbes (Fu et al. 2005); similarly, earthworms can increase carbon mineralization by enhancing carbon activation but decrease the net carbon mineralization by protecting a higher proportion of the newly activated carbon (Zhang et al. 2013). (4) One component affects other components or processes in an undetectable way. For example, as the bacterial-feeding nematode is not only affected by its prey soil bacteria but also by its predators at the same time, the correlation between bacterial-feeding nematodes and soil bacteria may be weak (Wardle and Yeates 1993); however, the contribution of bacteria to bacterial-feeding nematodes cannot be ignored. (5) One component may "trap" most of the energy and nutrient within its own loop and allow small portion of the energy and nutrients to be converted into other components. For example, as bacteria do in the ocean (Jiao and Zheng 2011), soil bacteria may capture most of the labile carbon and recycle it within the bacterial loop; this internal recycling of energy and nutrient is self-serving and not helpful to the development of the whole food web. In contrast, soil fungi are not likely to form such large internal loops but transfer more energy and nutrient to other components.

The summary of these major relationships in the plant-soil system may be a real start that we can investigate the complex system with a holistic approach.

In general, the impact of one component on other components or processes may be only in a certain range. Hence, if the change of one component or process exceeds its threshold, the related components or processes may not change accordingly if the related plant or soil biota does not necessarily evolve to adapt the new situation, or still change accordingly if the related plant or soil biota evolve successfully under such pressure/driver, or even change inversely if the related plant or soil biota cannot sustain normal metabolism. It is also notable that the high spatial and temporal heterogeneity in field soils provides a vast array of opportunity and refuge for soil biota and, thus sustain higher biodiversity and various distinct processes at different scales. Therefore, the field soil system is theoretically more stable or could recover more rapidly than microcosm soil systems in the lab, that is to say a lab microcosm study is likely to overstate the effects. This will be a major obstacle for scaling up the results from a microcosm study to field, regional and global scales. Unfortunately, given that the five major relationships occur together, the actual role of a given component in plant-soil system is hard to separate from the others, especially in field experiments. Microcosm studies in lab still provide a useful approach to quantify selected important processes which may be overridden by other processes in field. Nevertheless, new techniques are urgently needed to overcome the intrinsic limitations of a reductionist approach. For instance, the DNA stable isotope probing (DNA-SIP) in conjunction with metagenomics is useful to link microbial identity to particular metabolic functions and ecological processes (Chen and Murrell 2010). In addition, the process synthesis-based intact approaches such as the barometric process separation (BaPS) method, which has been proposed to measure soil gross nitrification rate (Ingwersen et al. 1999), and the holistic statistical tools such as Structural Equation Modeling (SEM) (de Vries et al. 2012) are worthy of development.

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